SYSTEMATICS AND EVOLUTION OF THE BRACHIOPODS "PACHYMAGAS" AND WAIPARIA IN NEW ZEALAND

A thesis

submitted in partial fulfilment

of the requirements for the Degree

of

Master of Science in Geology

in the

University of Canterbury

by

S. Fryer

University of Canterbury

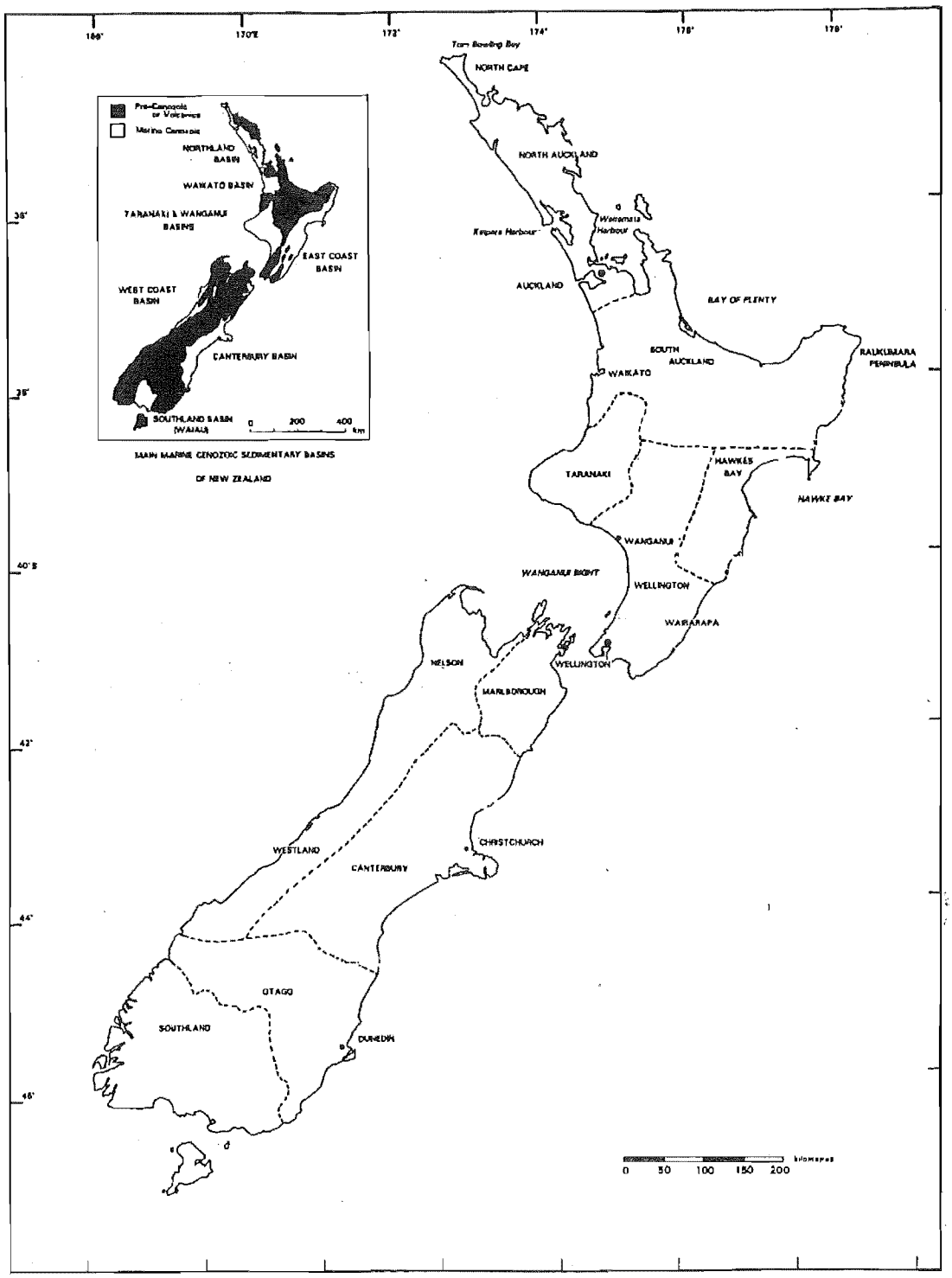
1999

Table of Contents

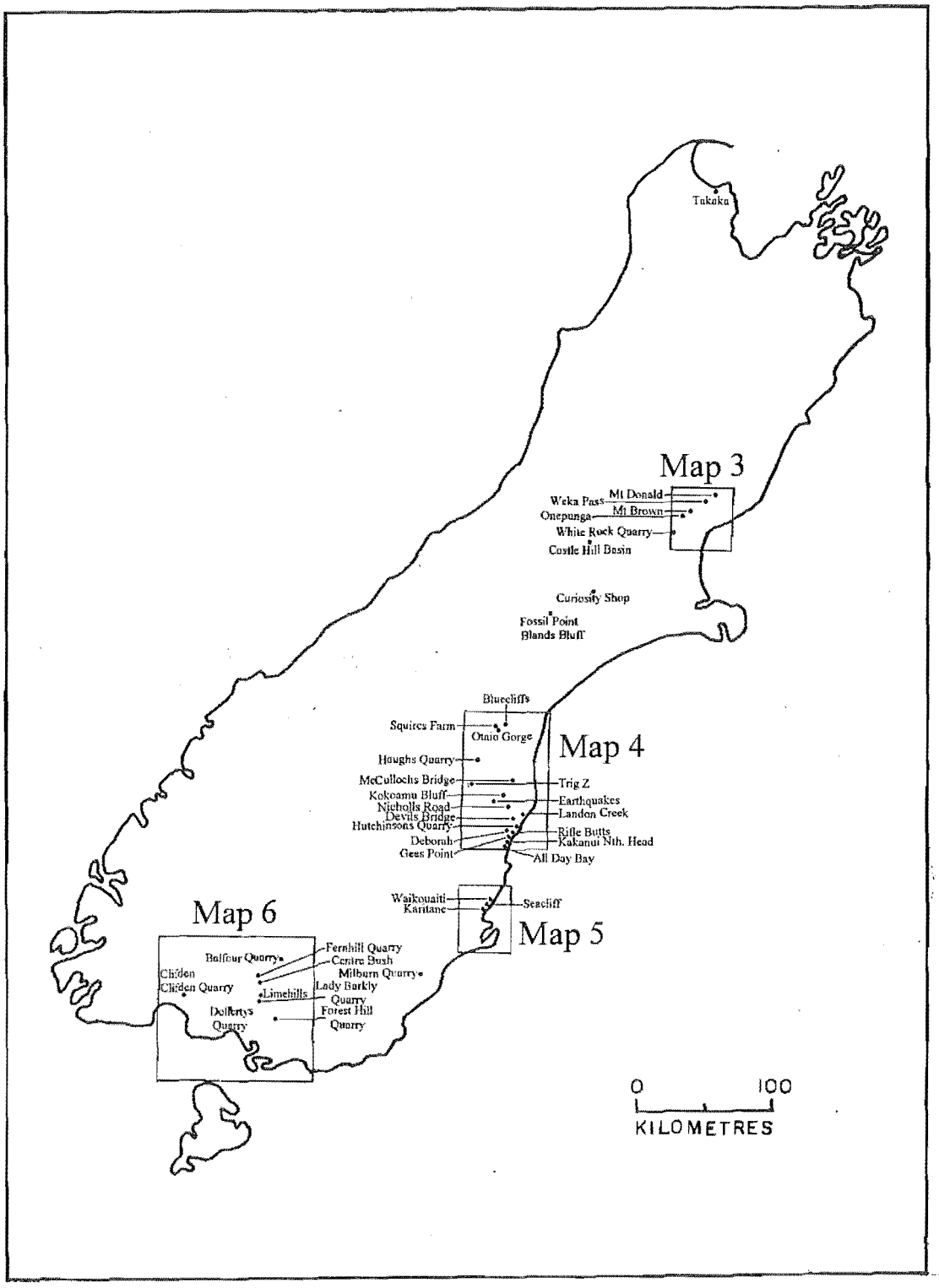
Chapter Two

Chapter Three

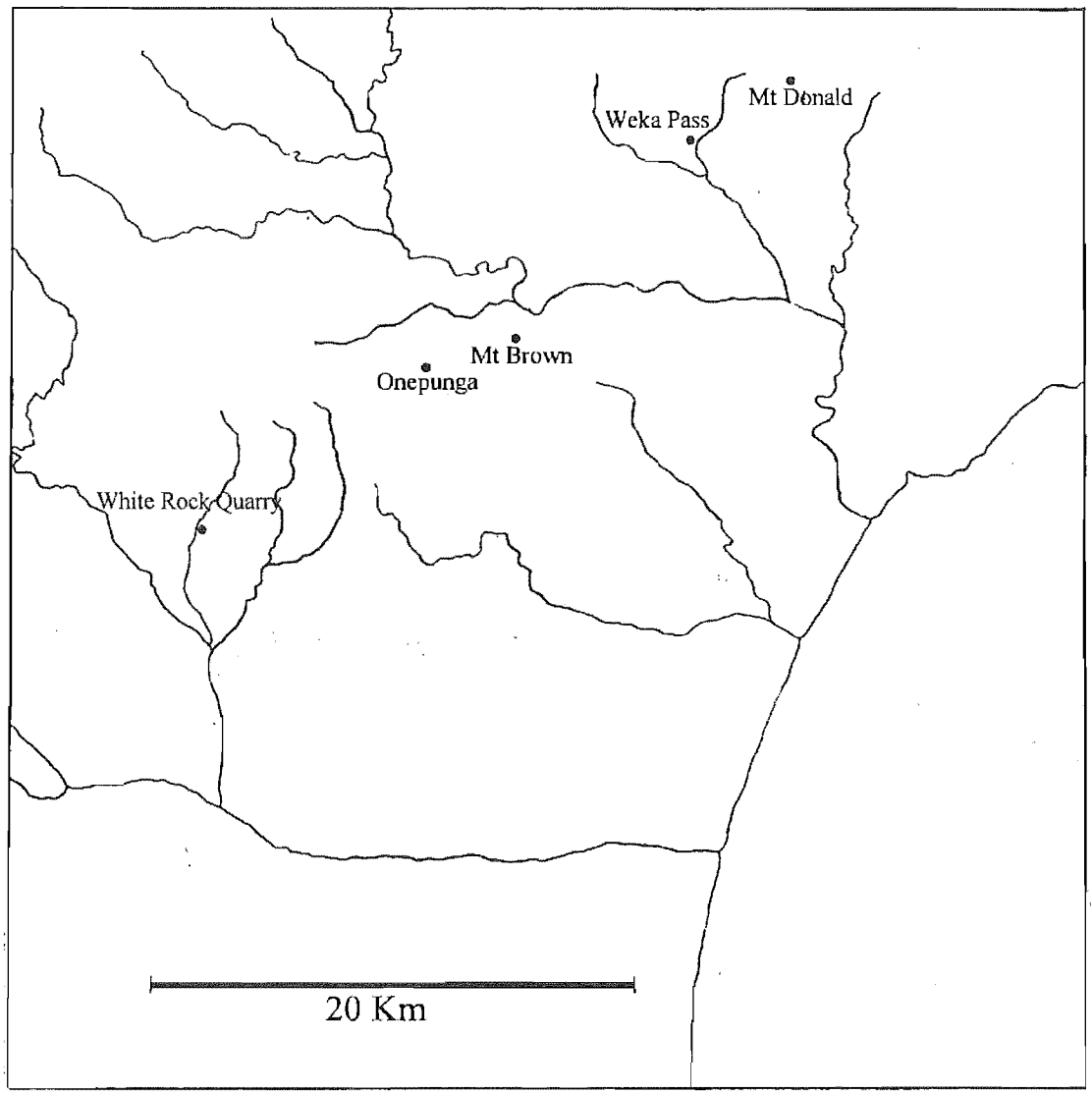
List of Tables and Figures



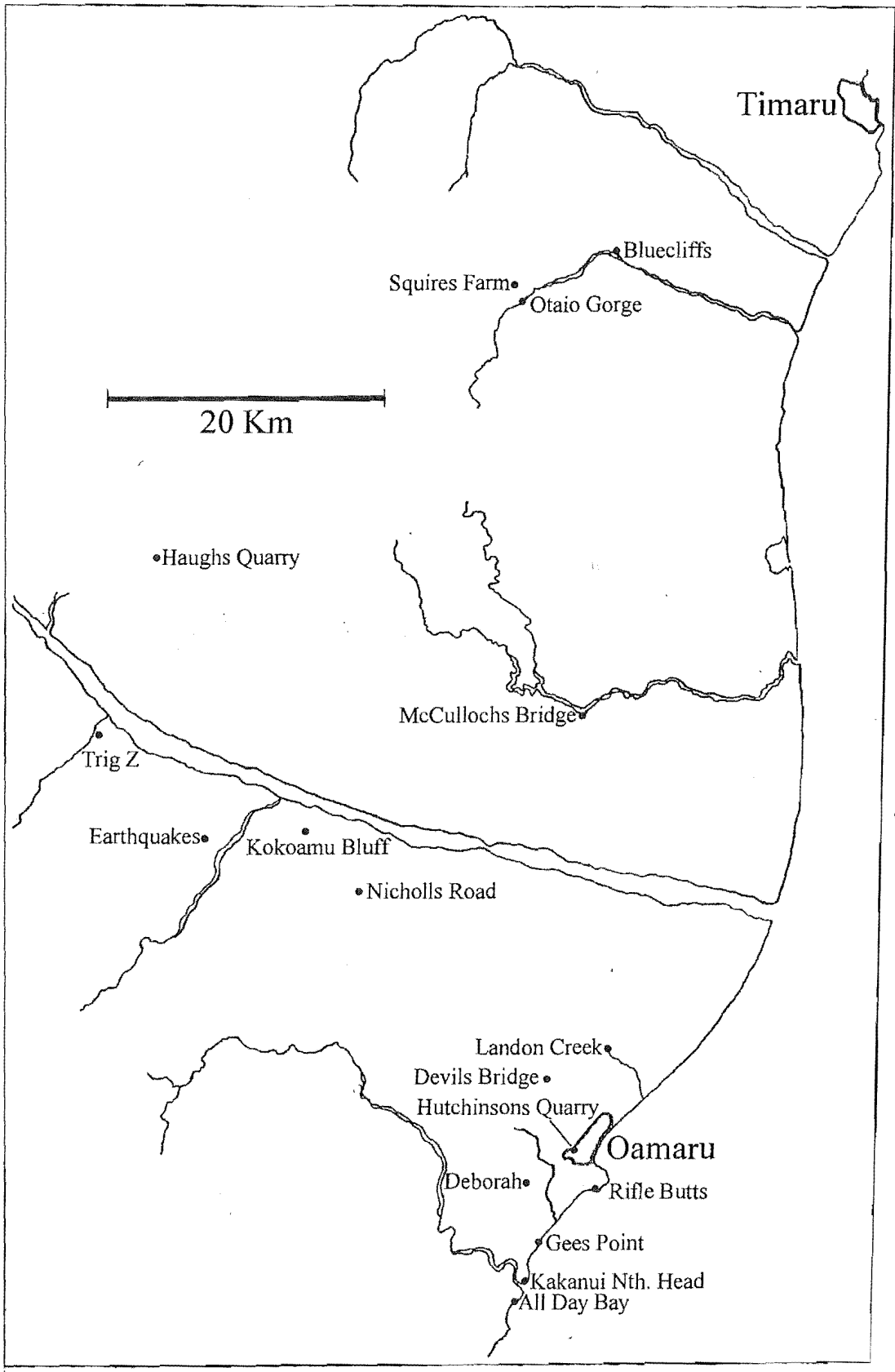
Map 1. Maps of New Zealand showing main marine Cenozoic sedimentary basins (top left inset) and North and South Island Provinces. (Modified from Hornibrook et al. 1989)



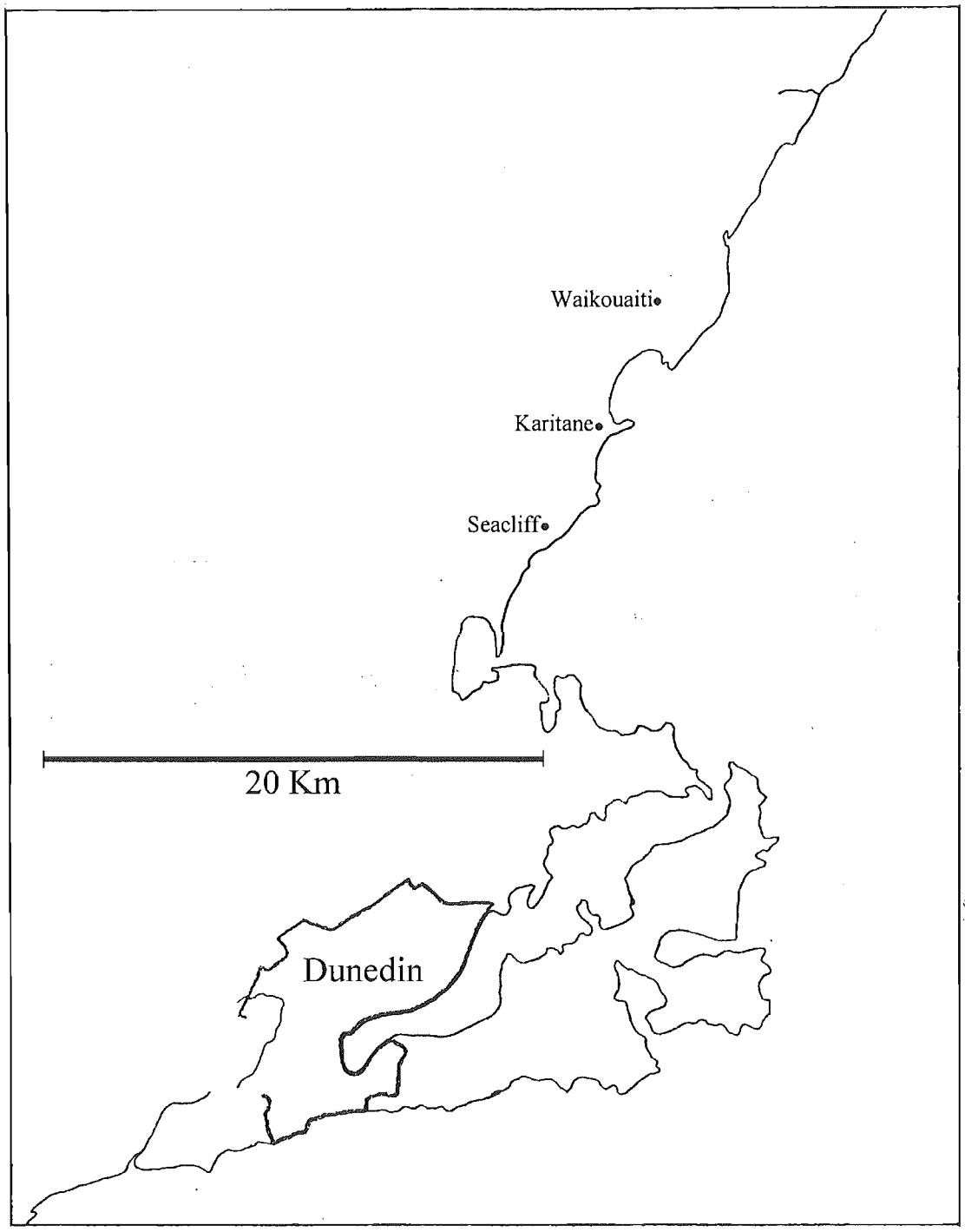
Map 2. Important South Island localities of this study with areas covered by smaller scale maps framed. (Modified after Bowen & Campbell 1973).



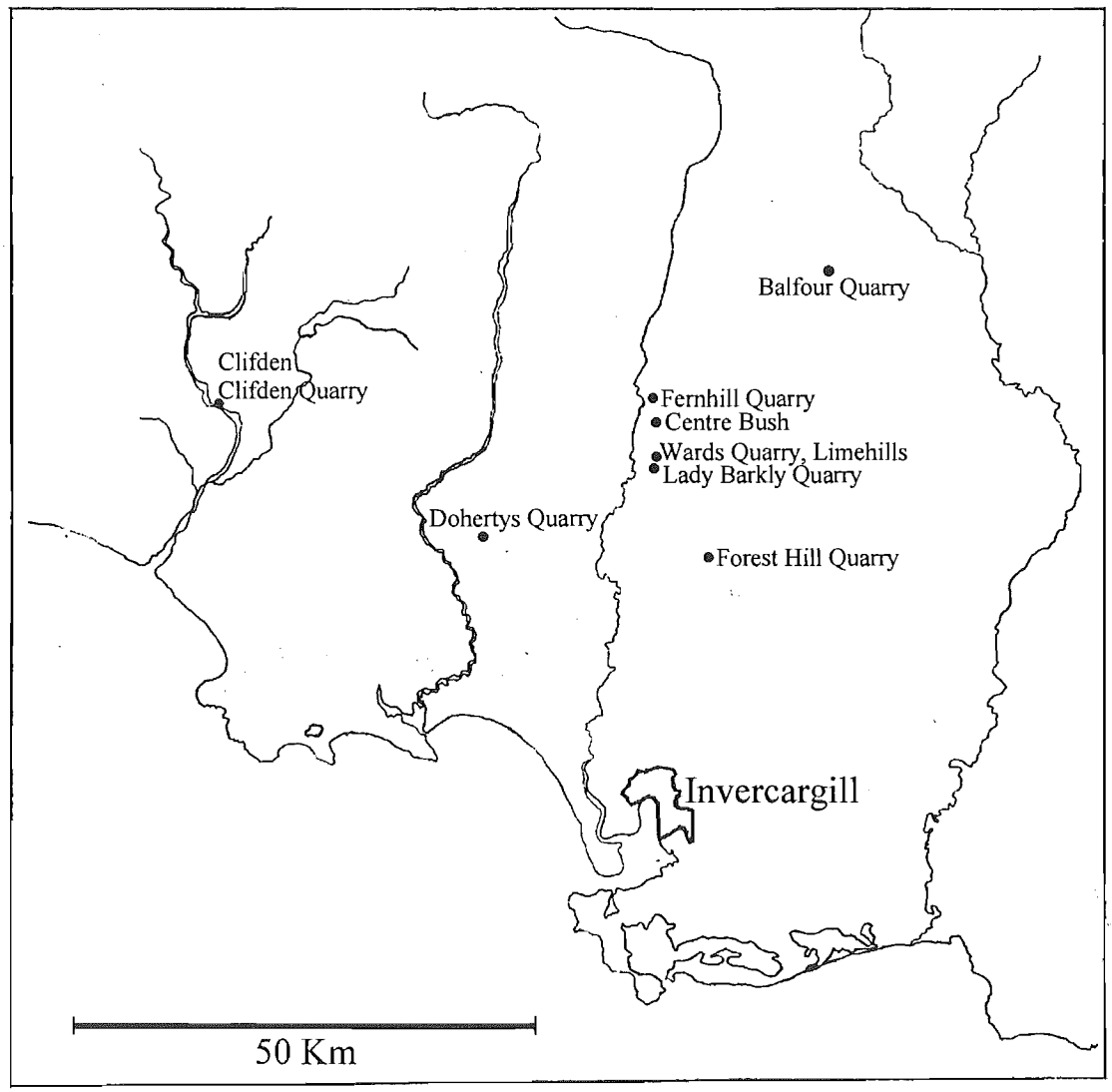
Map 3. Important North Canterbury localities of this study. (Modified after McCulloch 1981)



Map 4. Important North Otago localities of this study. (Modified after Lee et al 1996 and Fordyce et al 1985)



Map 5. Important localities of this study in the vicinity of Dunedin. (Modified after Cooper 1966)



Map 6. Important Southland localities of this study. (Modified after Willett 1950)

Abstract

New Zealand brachiopod species previously referred to *Pachymagas* and the associated genus *Waiparia* are systematically revised, the profusion of questionably substantiated species names and the inappropriate and untenable generic equivalence given (hence "*Pachymagas*" of the title) with younger, morphologically dissimilar South American species providing the rationale and impetus for the revision.

Through excavation to expose cardinal characters it was found that a relatively consistent morphology was retained throughout the "*Pachymagas*"-*Waiparia* lineage, the progressive thickening of the posterior of the shell interpreted to reflect the free-lying habit adopted, the thickening helping to weight the shell and hold it in a stable position on the substrate. Further, it was determined through examination of excavated interiors that at least two distinct genera have been placed in "*Pachymagas*"; a third distinct genus may also have been incorporated, but this possibility requires further study before any confident conclusions can be made.

Of the twenty-four species assigned to "*Pachymagas*" by previous authors, eight are recognised, one tentatively, with one new species erected. The extensive synonymisation required results from the typological species model employed in the creation of species by the two primary authors for the genus, J. A. Thomson and R. S. Allan. Both authors recognised many distinct species based on minor differences in exterior shape, but here it is considered that these species are rather phenotypic variates of a phenotypically plastic genus. Phenotypic variation is a far simpler explanation for the minor differences in shell shape that are observed within and between localities, and it affords well with the observation that interior characters are highly variable, the phenotypic variation being global in its expression.

The establishment of evolutionary relationships are compounded by the phenotypically plastic nature of "*Pachymagas*", the occurrence of ecophenotypes further blurring genotypic identity. However, it was determined that the evolutionary sequence can be considered a peramorphocline – a "sequence of increasingly more peramorphic species".

Chapter One:

'Background'

"Among the New Zealand Tertiary brachiopods, a host of species has been created by man, if not by nature, in a number of genera whose names are now well established in the literature. With further collecting at the classic localities, it has become increasingly evident that many of the species of genera such as "*Pachymagas*" (itself almost certainly not the same as the South American genus bearing that name but perhaps synonymous with Thomson's (1920) genus *Waiparia*), *Rhizothyris* (since skilfully analysed by Bowen and Campbell 1973), and *Liothyrella* may be better regarded as highly variable representatives, restricted in space and time, of but a few polymorphic species." (Dawson 1990a, p. 9).

1.0 Introduction

Brachiopods attributed to the genera *Waiparia* Thomson and *Pachymagas* von Ihering, described from New Zealand almost exclusively by the brachiopod workers J. A. Thomson and R. S. Allan, are a significant and highly visible component of mid-outer to inner shelf sands, limestones and calcareous greensands of late Oligocene to early Miocene ages along the east coast of the South Island of New Zealand. While *Waiparia* has been (see section 1.2) considered an exclusively New Zealand species, *Pachymagas* was first established (as a subgenus of *Terebratella*) and described from South American strata of Pliocene age (Ihering 1903). Thomson (1915) was the first to place New Zealand species within *Pachymagas*, considering the younger South American species more evolved representatives of the older New Zealand stock (Thomson 1927). Though Thomson (1920; 1927) did attempt to group the New Zealand and South American species into a number of nominally phylogenetic series, the evolutionary relationships between the various South American and New Zealand species have never been clearly or confidently expressed.

The most conspicuous feature of New Zealand *Pachymagas* to the present day brachiopod worker is the huge number of specific names assigned to the genus. The majority of these species come from but two localities and were discriminated solely on minor variations in exterior shape of the shell. The degree of variability in exterior shell shape *within* species was given little consideration, and never quantified. Indeed, characteristics of the interior were not often determined, the end result being tentative placement of some species within the genus and the incorporation of at least two dissimilar genera within New Zealand *Pachymagas*.

Matters of classification are further compounded for the present day worker in that Thomson's specific determinations for *Pachymagas* (plus, at least, *Rhizothyris*) were initially made under an inclusive species philosophy (e.g. Thomson 1918a), later changing to the more exclusive, typological species philosophy (e.g. Thomson 1920) that was followed by R. S. Allan. Specific determinations for *Pachymagas* made by Thomson and those adhering to his earlier (pre Thomson 1920) classification are sometimes hard to resolve or equate with species of the later (post Thomson 1920) classification. The typological species philosophy adopted by both Thomson and Allan is responsible for the present profusion of species names for New Zealand *Pachymagas*, the subtleties of discrimination of the various established species being such that little faith can be placed in identifications made by other contemporary workers, or indeed in the identifications of either of the two primary authors because variability in the species was not examined in any rigorous way.

It has been clear for many years that, for New Zealand, species of *Pachymagas* and the associated genus *Waiparia* need to be reassessed taxonomically, as Allan (1960; 1963) himself indicated. Though Allan (1949) noted the New Zealand

species of *Pachymagas* were not closely related to the South American *Pachymagas*, and thereafter (Allan 1957; 1960) referring to the New Zealand genus as "*Pachymagas*", the species have neither been reassigned to any existing genus nor have had a new genus erected for them. This study sets out to taxonomically reassess species assigned to "*Pachymagas*" and *Waiparia*, and to assign them a place within new or existing genera as the case may be.

1.1 Aim of Study

The aim of this study was ultimately to 'correct' the systematics of species established under an outdated typological species framework. More specifically, in addition to examination of specimens from the type localities of all the species (those that can be definitely placed, at least), a critical examination of the variability at those localities from whence great numbers of species had been described was a crucial aim. It was additionally an objective to examine brachiopod interiors for all the species under revision, not only to complement many previously inadequate descriptions, but to examine the variability of the cardinal features. This was important to establish the veracity of some of Thomson's "advanced"/"primitive" ascriptions for the cardinal processes of such species as *Pachymagas parki* and *P. haasti*. Establishment of the nature of the terebratelloid loop was also a consideration in the excavation of some specimens. It was also a major aim to establish phylogenetic relationships between the various species, and attempt to describe the evolution of the genus. Finally, it was desired to formally abandon the use of the generic name "*Pachymagas*" for New Zealand species, placing them instead in *Waitakia* gen. nov. (page 74) in recognition of their generic distinctness from the South American genus.

1.2 Scope of Study

It was implicitly intended that this study be limited to examination of New Zealand brachiopoda, as the two genera set out to be reinvestigated were thought to be endemic. However, Dr. D. I. MacKinnon brought to my attention brachiopods from King George Island off the Antarctic Peninsula, described as *Pachymagas* cf. *cottoni* by Biernat et al. (1985). The species in question looks very similar to *Waiparia abnormis* Thomson, though probably possesses a teloform loop (Fig. 1.). However, Biernat et al. (1985) found that two of their eleven sectioned specimens appeared to possess a trabecular loop. It may be the case that the majority of adult shells lose the connecting band; the species may represent a transition from trabecular to teloform stage of loop development. The degree of posterior shell thickening of the interior appears to be greater than in *W. abnormis* – a condition consistent with the more advanced state of loop development in the Antarctic species. Dr. D. I. MacKinnon postulates (pers. comm. 1998) that this species possibly evolved from an ancestral New Zealand form transported via the circum-antarctic current in the Early Miocene.

Another Antarctic species, *Pachymagas antarcticus* Buckman 1910, was withdrawn from that genus and placed in *Magellania* by Owen (1980), and therefore lies outside the scope of this study. Though the Patagonian species of *Pachymagas* also lie outside the scope of this study, comparison of *Pachymagas tehuelcha* with New Zealand species previously referred to that genus is made in section 1.6 to highlight the significant differences that make generic separation necessary.

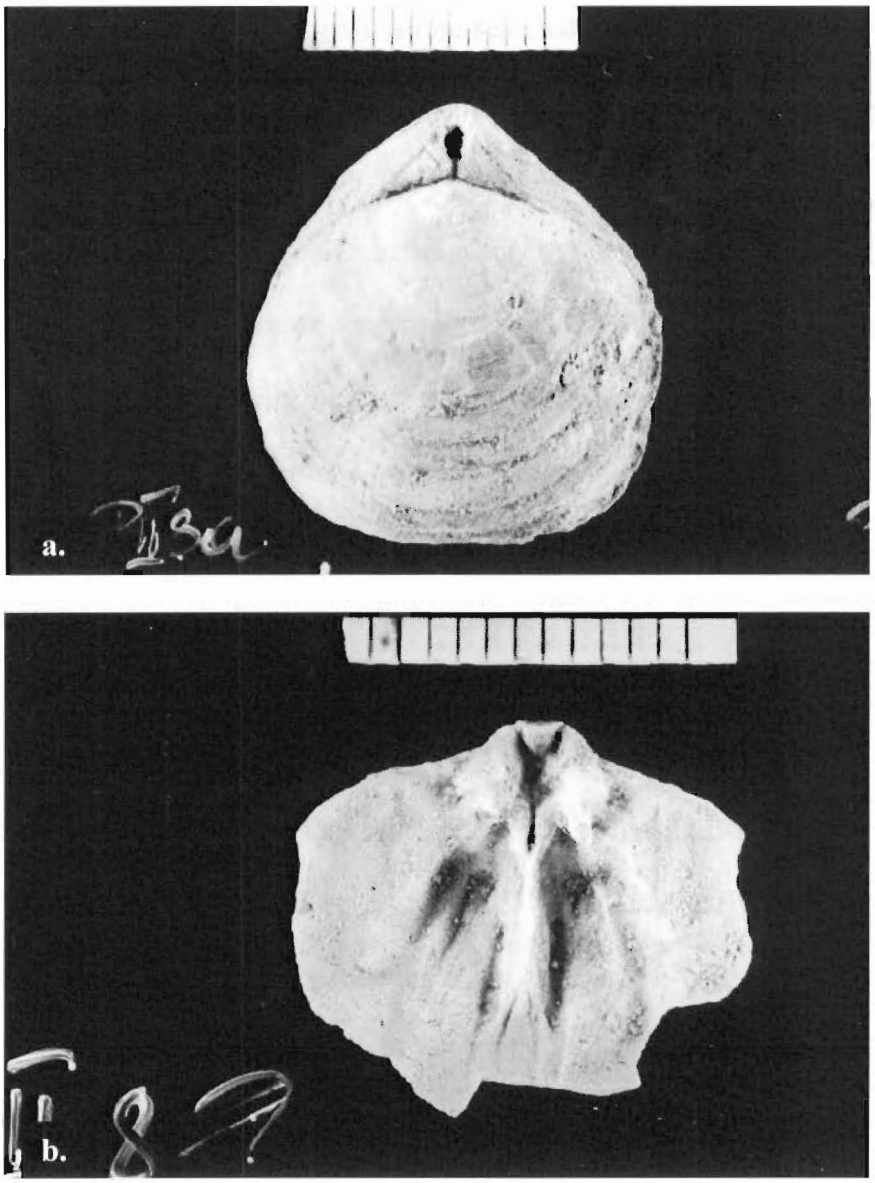


Figure 1. *Pachymagas* cf. *cottoni* of Biernat et al. (1985). Reproduced from original figures.

1.3 Methods of Study

In aid of partially quantifying variation, selected dimensions and characters of the exterior were measured with a vernier calliper or otherwise recorded for later use in graphical analysis. Where necessary, some localities were recollected, especially established 'classic' brachiopod localities, often for fragments demonstrating interiors or for supplementary statistical examination. Extensive excavation of some specimens from collections at the University of Canterbury was carried out under a binocular microscope and using a fine needle. Specific searches during fieldwork for dorsal valve fragments displaying well preserved cardinalia supplemented investigation as, for most localities, the matrix was well indurated, making successful excavation difficult.

While it is well recognised that biometric study of fossils is a less than totally satisfactory ideal (e.g. Scott 1980), a decision was made early that simplistic statistical measures were probably adequate for the study. This was especially considered to be the case as more involved methods such as scanning specimen images, then calculating their outlines (Scott 1980) on a computer, were time consuming, and there was no guarantee that the information attained would be of a value above that of more simplistic techniques. It was considered that a statistical treatment such as that successfully carried out in the systematic revaluation of *Rhizothyris* (Bowen & Campbell 1973) would equally well suffice for *Waiparia* and *Waitakia*.

1.3.1 Characteristics Recorded

The characteristics recorded, and dimensions measured follow, with their abbreviated forms (as used in Appendix) in brackets:

Ventral Valve Length (Length v): the longitudinal length taken from the beak to the anterior edge of the valve (see fig. 2).

Dorsal Valve Length (Length d): the longitudinal length taken from the cardinal margin to the anterior edge of the valve (see fig. 2).

Maximum Thickness (Thickness max.): the maximum thickness measured orthogonally to the commissural plane (see fig. 2).

Maximum Width (Width max.): the maximum width of the shell, measured orthogonal to valve length (q.v.) in the plane of the commissure (see fig. 2).

Ventral Valve Length at Maximum Width (Lth. v@Wmax.): the longitudinal length taken from the beak to the point of Maximum Width (q.v.) (see fig. 2).

Beak Curvature (Beak Curvature): classified according to Thomson's (1927, p. 80, fig. 23) scheme (see fig. 3 and subsection 1.3.2 below). Assigned relative values in Appendix as follows:

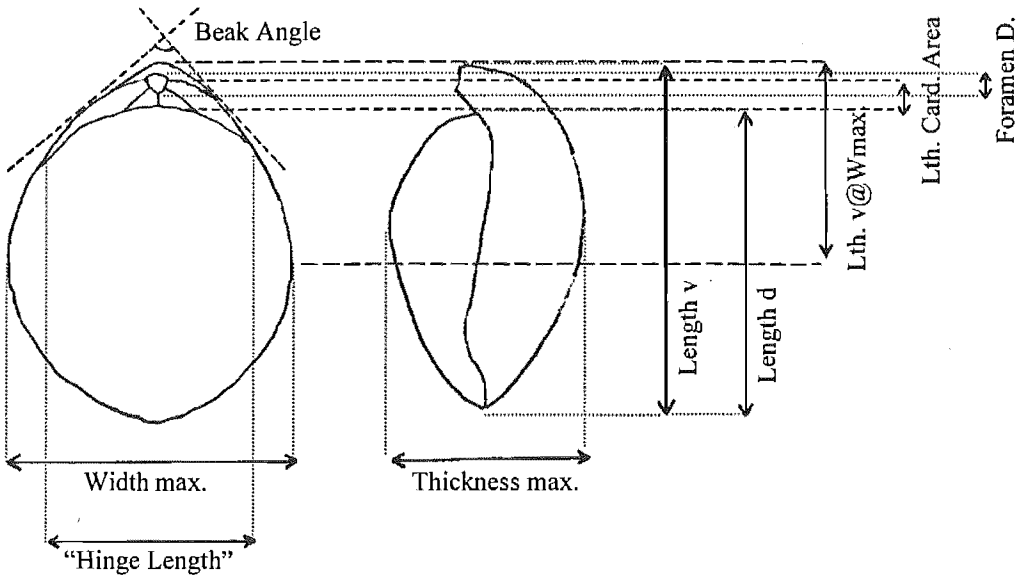


Figure 2. Diagram demonstrating the various measures that were taken for statistical analysis, and as used in Appendix (refer to main text for unabbreviated word forms).

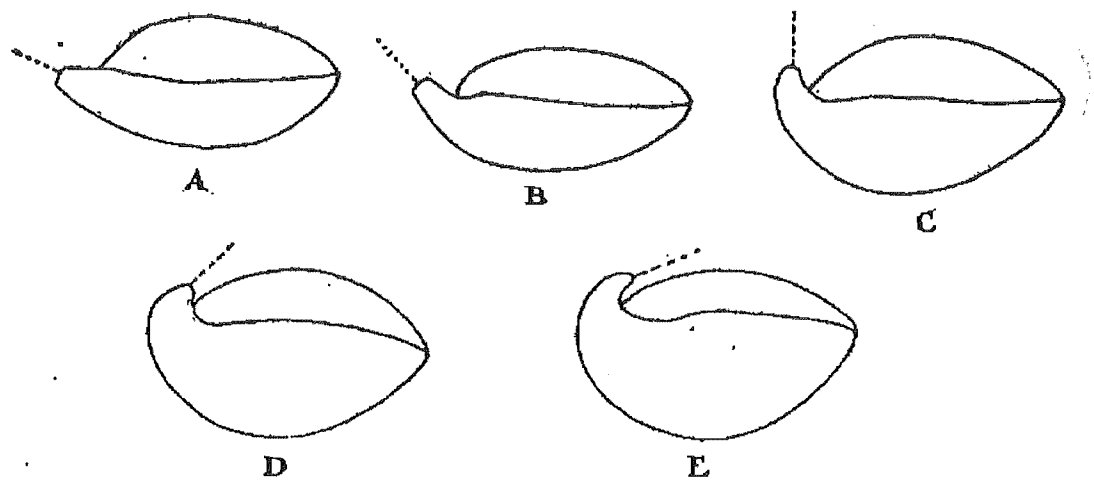


Figure 3. Diagram demonstrating degrees of beak curvature. **a**. Nearly Straight. **b**. Suberect. **c**. Erect. **d**. Slightly Incurved. **e**. Strongly Incurved. (From Thomson 1927)

Curvature Index	Descriptor
1	Nearly Straight
2	Suberect
3	Erect
4	Slightly Incurved
5	Strongly Incurved

Table 1. Beak Curvature.

Length of Cardinal Area (Lth. Card. Area): measured longitudinally from the cardinal margin to the intersection point of the beak ridges with the foramen. This measure varies with the type of foramen involved, as the beak ridges meet above the foramen in hypothyrid specimens, for example (figure 2 and see section 1.3.2).

Beak Angle (Beak Angle): measured tangentially about the beak (see fig. 2).

"Hinge Length" ("Hinge Length"): the lateral length measured between the points at which the dorsal valve first onlaps the ventral valve (see fig. 2).

Foramen Diameter (Foramen D.): the 'length' of the foramen; measured longitudinally (see fig. 2).

Foramen Type (Foramen Type): classified according to Thomson's (1927, p. 71-73, fig. 20) scheme (see fig. 4 and subsection 1.3.2 below).

Sulcation Index (Sulcation Index): arbitrarily defined categories of relative sulcation assigned numerical values (see fig. 5) in Appendix as follows:

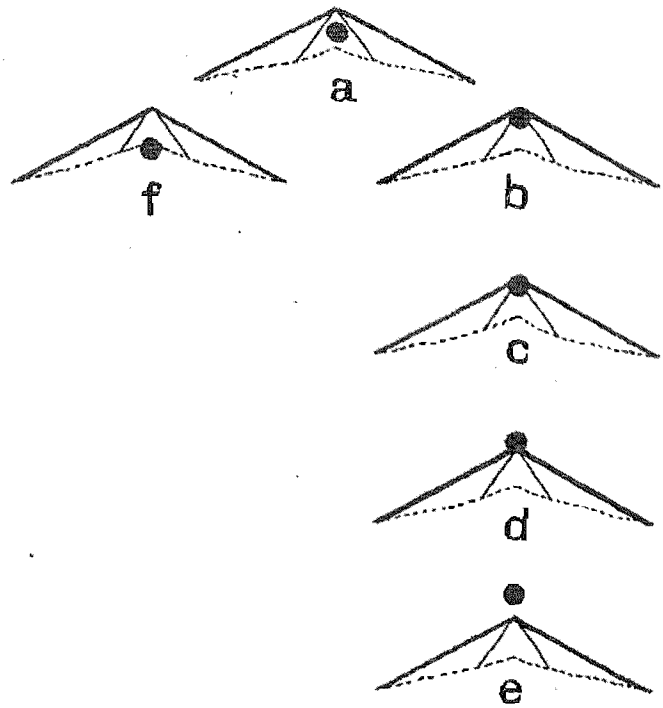


Figure 4. Position of the foramen is shown above. The foramen is represented by the filled circle, while the heavy lines represent the line of the beak ridges. The dotted lines show the line of the cardinal margin. **a.** hypothyrid foramen. **b.** submesothyrid foramen. **c.** mesothyrid foramen. **d.** permesothyrid foramen. **e.** epithyrid foramen. **f.** amphithyrid foramen. (From Thomson 1927)

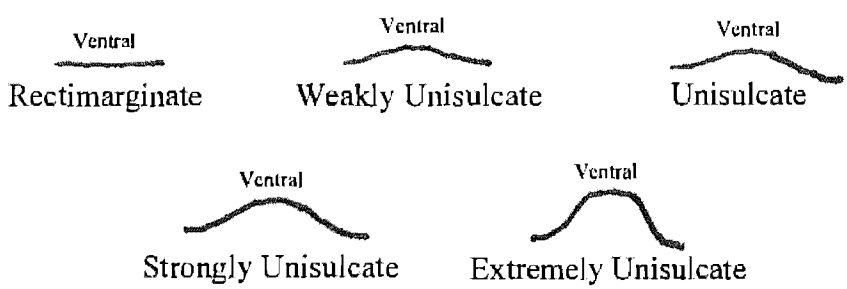


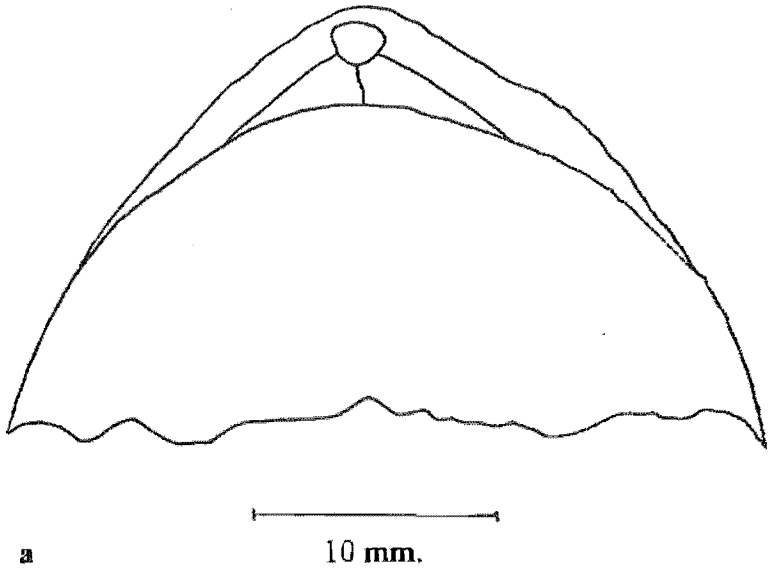
Figure 5. Diagram demonstrating the degree of sulcation of the anterior commissure, and the discontinuous categories used in this study. The diagrams are shown with the ventral valve uppermost.

Sulcation Index	Descriptor
0	Rectimarginate
0.5	Incipiently Sulcate
1	Weakly Sulcate
2	Sulcate
3	Strongly Sulcate
4	Extremely Sulcate

Table 2. Sulcation Index.

1.3.2 Beak Curvature (ref. fig. 6, fig. 7)

Throughout this work, terms describing the degree of beak curvature are taken as proffered by Thomson (1927, p. 80, fig. 23). However, it was found that this scheme was open to a deal of confused application in regard to brachiopods with significantly different foramina, e.g. *Waiparia abnormis* and *Waitakia haasti*. For this study, the problem lay in applying Thomson's terminology in a consistent manner amongst brachiopods possessing submesothyrid and hypothyrid (as opposed to mesothyrid) foramina. In Thomson's figure (1927, p. 80, fig. 23; reproduced here as fig. 3), the illustrations represent specimens where the angle the pedicle would have made with the commissural plane is the true indicator of how curved the beak is; or at least whether the specimen should be designated erect, suberect, incurved, etc. Hence, it is the angle of projection of the pedicle with regard to the commissural plane rather than seeming beak curvature noted in profile that should be used to define curvature, because this metric can be used in a consistent manner among brachiopods with differing foramen types. As shown in figure 6 and 7, the profiles of *W. haasti* and *W. abnormis* look markedly similar, but when the angle at which the pedicle would have projected from the ventral valve is marked in, the true difference in 'beak curvature'



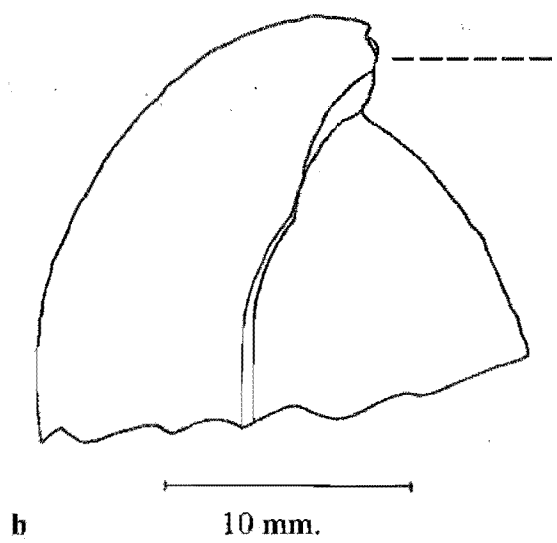
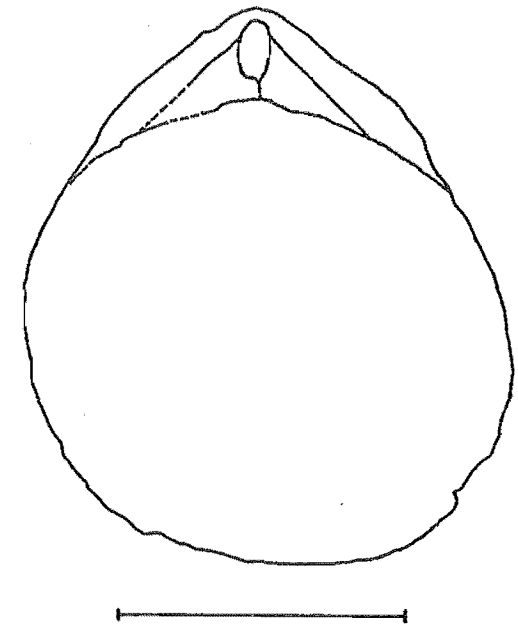
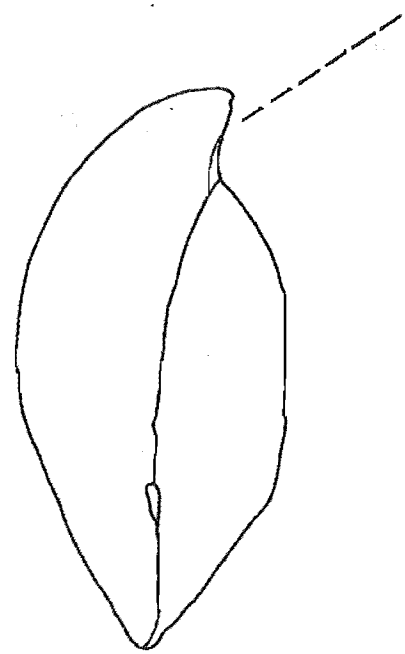


Figure 6. Diagrams illustrating *W. haasti* (Allan Collection specimen 26947; Canterbury University). **a.** View demonstrating the mesothyrid foramen (anterior portion of shell not depicted). **b.** View demonstrating the angle at which the pedicle would have projected from the beak. This specimen has an *erect* beak (see fig. 3).



a 10 mm.



b 10 mm.

Figure 7. Diagrams illustrating *W. abnormis* (specimen UCM 2031; Canterbury University). **a.** View demonstrating the hypothyrid foramen. **b.** View demonstrating the angle at which the pedicle would have projected from the seemingly erect beak. This specimen is *suberect* (see fig. 3).

is revealed. It is important to record correctly such beak curvatures, as functionality of the pedicle is therein reflected.

1.4 Thesis Organisation and Conventions

This thesis is organised into four chapters – Chapter One: 'Background', containing a brief introduction, discussion of the establishment and modification of pertinent New Zealand Stage names, and explaining the aim, scope, and methods of the current study; Chapter Two: 'Historic Works', covering the published literature and interpretations of the two brachiopod workers largely responsible for systematic description and phylogenetic interpretation of "*Pachymagas*" and *Waiparia*; Chapter Three: 'Systematic Palaeontology', wherein the species of this study are fully described, discussed, and figured; Chapter Four: 'Discussion and Conclusions', the results of the study are analysed and discussed, conclusions made and future work suggested. An Appendix follows Chapter Four and contains measurements made for numerous brachiopods from various localities, used in this study to construct the graphs found in Chapter Three. A list of references follows the Appendix.

There are three main conventions followed in this study, the first being to enclose personal comment within the body of a quotation within square brackets – "...there is a higher division present [within the greensands] containing...". The second convention used is to place redundant stage names within parentheses – "Hutchinsonian". The final convention is to follow redundant names with the new names of this study in brackets – *Pachymagas andrewi* (*Waitakia andrewi*).

While not a convention as such, it should be noted that specimens referred to as coming from the "Allan Collection" or "Allan Colln." come from the Allan Brachiopod Collection in the Department of Geological Sciences, University of Canterbury. Specimens referred to in the text as "UCM" likewise come from Canterbury University, from the University of Canterbury Macrofossil collection.

1.5 New Zealand Stages

N.B. To aid in comprehension, reference should be made to tables 3, 4, and 6.

New Zealand stage names have arisen, been replaced and revised throughout the history of geological investigation from 1916, when Thomson first sought to classify strata of the New Zealand Middle Tertiary. This discussion deals with only a few stage names – those that have been subdivided, replaced and changed significantly since their original establishment, and to which "Pachymagas" and Waiparia have been recorded as occurring. In this work, stages that are redundant are enclosed in quotation marks (see section 1.4) e.g., "Hutchinsonian" – a stage now incorporated into the Altonian. However, for clarity, this convention has not been used in *this* section. Tables 3 and 4 summarise the important changes that occurred to the subdivision of the New Zealand Tertiary over a period of approximately seventy years, beginning with the first formal attempt at classification by Thomson (1916). The present divisions of the Tertiary are demonstrated in table 5.

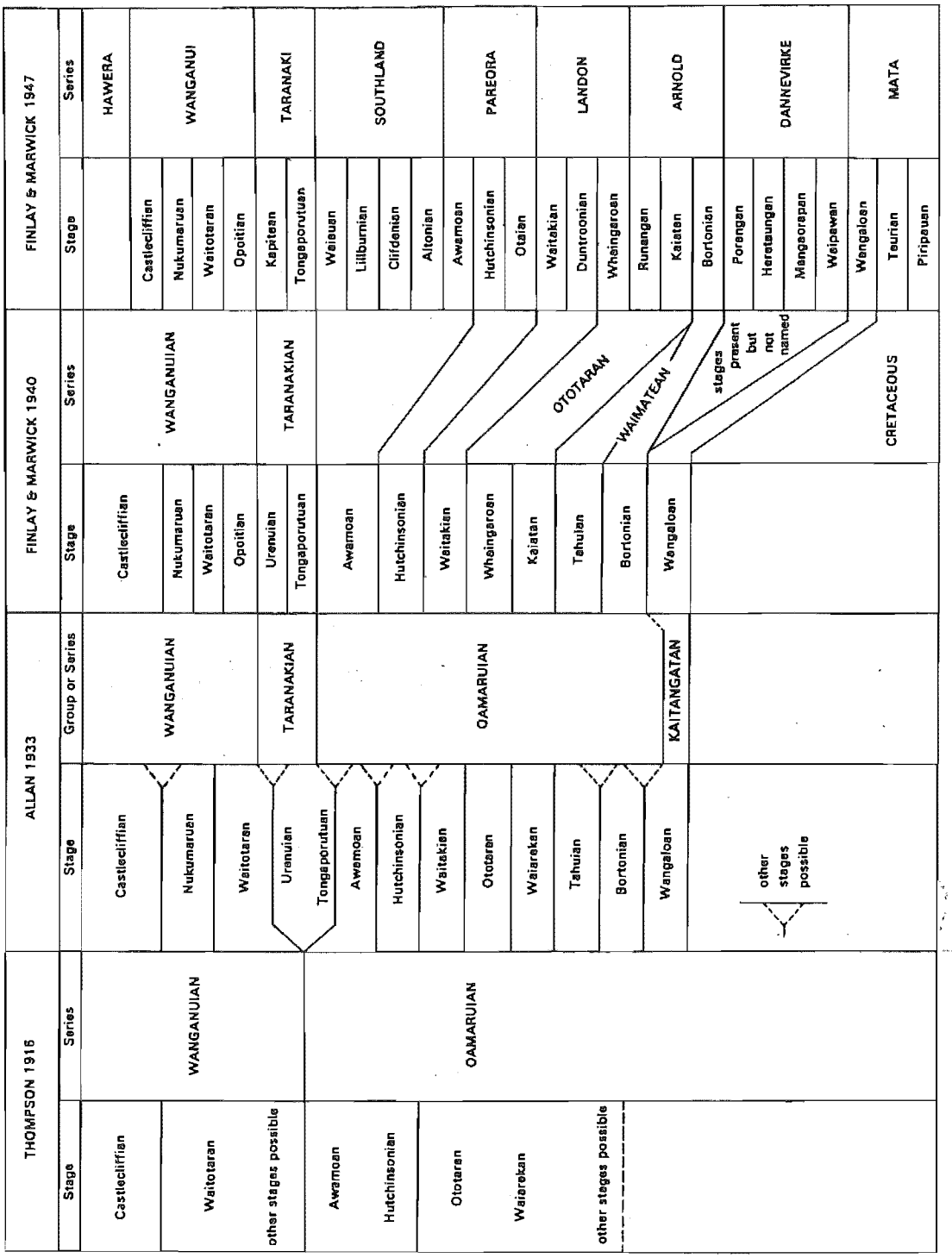


Table 3. History of the development of the New Zealand stages from 1916 to 1947 (From Hoskins 1982).

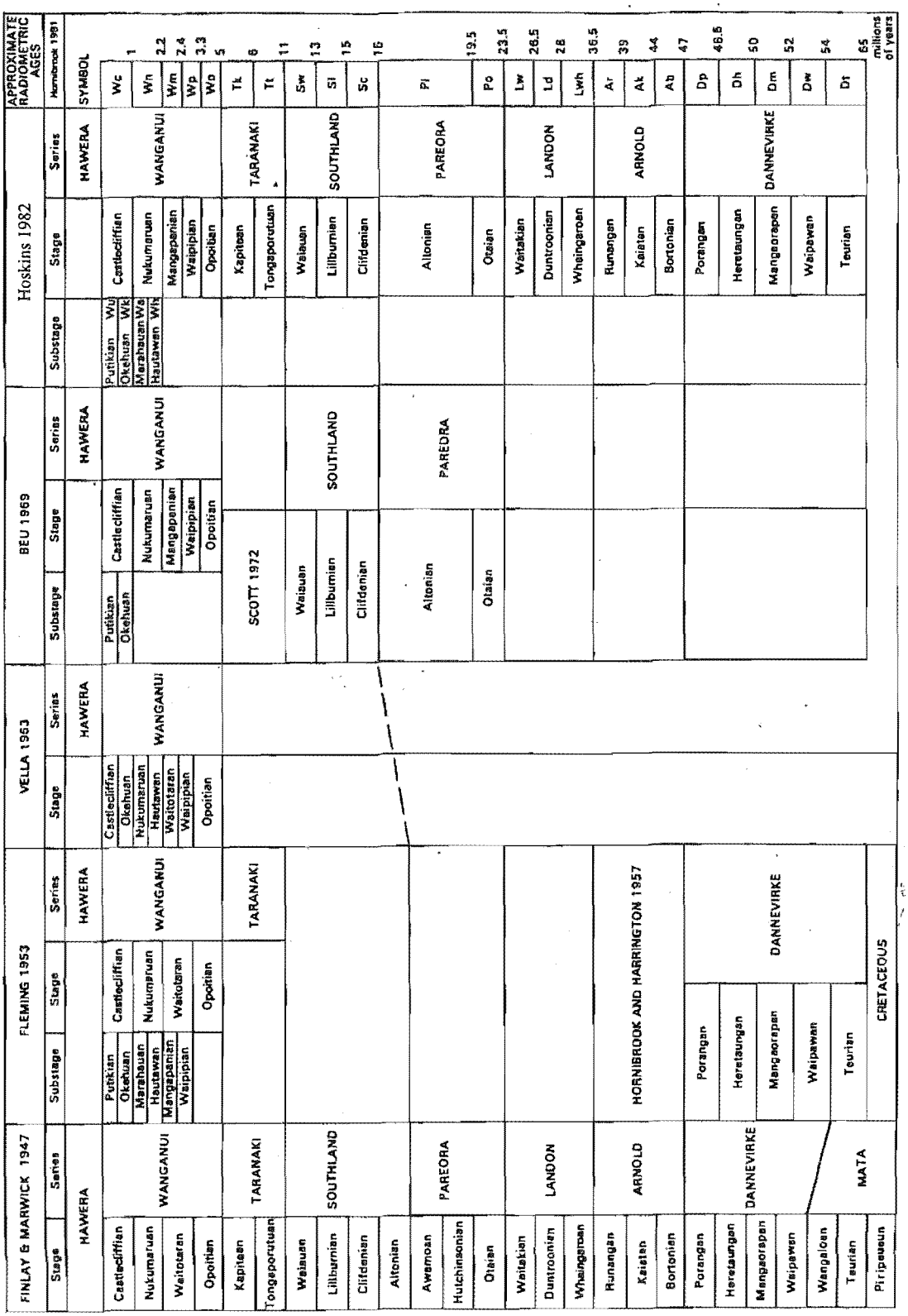
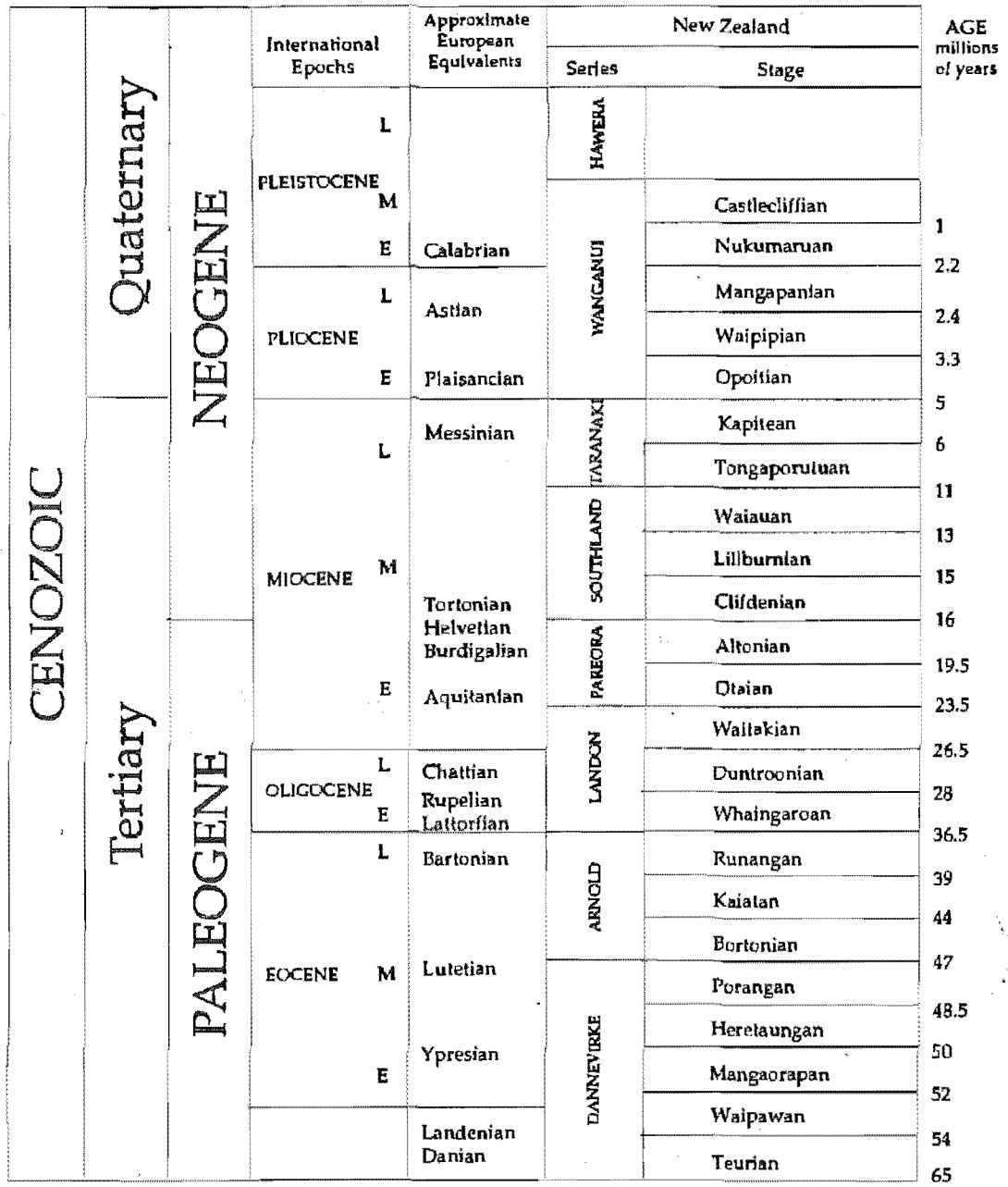


Table 4. History of the development of the New Zealand stages from 1947 to 1982 (Modified from Hoskins 1982).



			International Epochs		Approximate European Equivalents	New Zealand Series	New Zealand Stage	AGE millions of years
CENOZOIC	Quaternary	NEOGENE	PLEISTOCENE	L		HAWERA		
				M		WANGANUI	Castlecliffian	1
				E	Calabrian		Nukumaruan	2.2
			PLIOCENE	L	Astian		Mangapanian	2.4
				E	Plaisancian		Waipipian	3.3
							Opoitian	5
	Tertiary		MIOCENE	L	Messinian	TARANAKI	Kapitean	6
							Tongaporutuan	11
						SOUTHLAND	Waiauan	13
				M			Lillburnian	15
					Tortonian Helvetian Burdigalian		Clifdenian	16
		PALEOGENE				PAREORA	Altonian	19.5
				E	Aquitanian		Otaian	23.5
						LANDON	Waitakian	26.5
			OLIGOCENE	L	Chattian		Duntroonian	28
				E	Rupelian Lattorfian		Whaingaroan	36.5
			EOCENE	L	Bartonian	ARNOLD	Runangan	39
							Kaiatan	44
				M	Lutetian		Bortonian	47
						DANNEVIRKE	Porangan	48.5
							Heretaungan	50
				E	Ypresian		Mangaorapan	52
							Waipawan	54
					Landenian Danian		Teurian	65

Table 5. Present divisions of the New Zealand Tertiary and Quaternary (From Dawson 1990a).

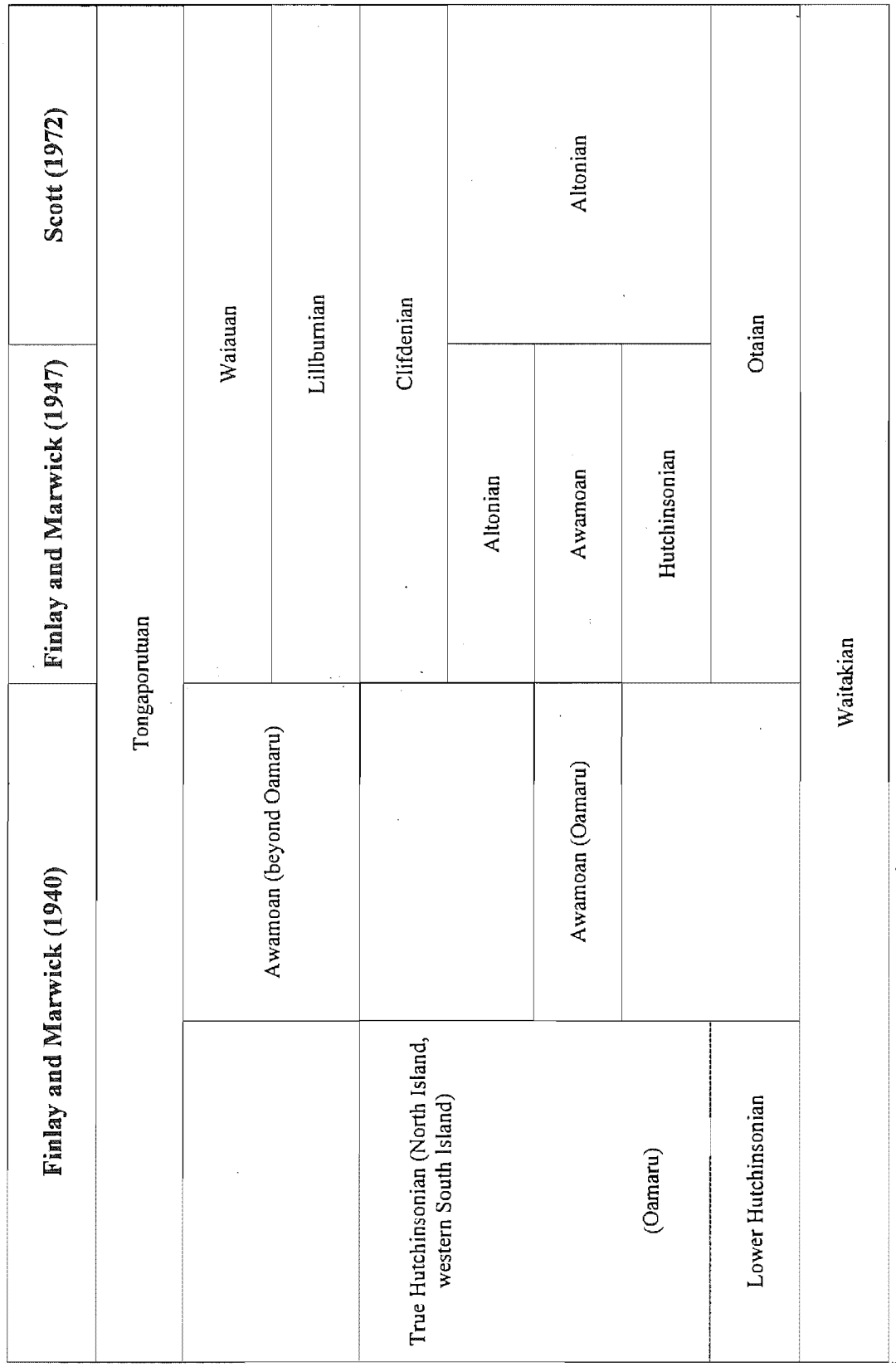


Table 6. Diagram illustrating both the inadvertent expansion of the Hutchinsonian Stage due to correlation with strata outside of the Oamaru district, and the erroneous Awamoan age given to strata latter classified as Lillburnian and Waiauan beyond Oamaru. (Modified after Scott 1971)

1.5.1 Duntroonian and Waitakian

The Duntroonian Stage was established by Allan (1938b) for strata bearing the *Liothyrella landonensis* fauna, with the type locality at Landon Creek; the Waitakian initially an upper substage of the Hutchinsonian proposed by Park (1918) for the "...glauconitic calcareous sandstone that forms the Waitaki stone [Otekaike Limestone]..." (Park 1918, p. 25). Allan (1933), noting that the Waitaki limestone (Otekaike Limestone) contained a pre-Hutchinsonian brachiopod fauna, argued that the Waitakian had to be redefined: "The Waitakian may be defined as the interval of time represented by the deposition of the Waitaki limestone and the Otaike beds of the Waitaki Valley, and as well such periods as may be represented therein by non-deposition or erosion." (Allan 1933, p. 98). Trig Z, Otaike, was selected as the type locality.

Both of these stages as defined by Allan have stood the test of time. However, Finlay & Marwick (1940) did initially relegate the Duntroonian to a substage of the Waitakian, Finlay having suggested the two stages were only separable zones on brachiopod and mollusc evidence (Finlay 1939a, p. 508). These authors later (Finlay & Marwick 1947, p. 229) included the Duntroonian in their table demonstrating divisions of the New Zealand Upper Cretaceous and Tertiary.

1.5.2 Otaian

The Otaian Stage was introduced by Finlay & Marwick (1947) . It was defined on foraminifera, the type locality at Blue Cliffs, on the Otaio River. The stage accommodated the Lower Hutchinsonian (Finlay 1939a; Finlay & Marwick 1940)

greensands of the Oamaru coastal district, containing brachiopods "less advanced" than those of the Hutchinson's Quarry greensands themselves. Thomson (1926, p. 151) had suggested that the differences in aspect of the faunas of the two horizons might indicate a difference in age; Allan (1933) still retained these two distinct faunas in the Hutchinsonian, but did note that four faunal divisions of the Hutchinsonian Stage could be made – of which the "*Pachymagas parki* assemblage" and the "*Pachymagas hectori* assemblage" would now be placed in the Otaian.

1.5.3 Hutchinsonian, Awamoan, Altonian

Thomson (1916) proposed the Awamoan and Hutchinsonian Stages, defining them from strata of the Oamaru coastal district. The Hutchinsonian Thomson defined as the beds developed between the Ototara Limestone and the shell bed at Target Gully; the Awamoan for the "Awamoa beds" – Awamoa Creek evidently the intended type. Allan (1933), in an attempt to treat New Zealand stages more rigorously, formally recorded type localities; in this respect he stated that the strata exposed at Awamoa Creek were unsuitable for a standard because of isolation from rocks of similar age, and suggested that Rifle Butts should be considered the type locality, Thomson not having clearly presented a type. However, Finlay & Marwick (1940) rejected this suggestion, indicating that it was Thomson's intention that Awamoa Creek be the type. As has already been mentioned, Finlay & Marwick (1947) split the Hutchinsonian; the Lower Hutchinsonian (of Finlay & Marwick 1940) becoming the Otaian; the True Hutchinsonian (of Finlay & Marwick 1940) retained as the Hutchinsonian. Finlay & Marwick (1947) also introduced the Altonian Stage from strata at Clifden, defining it on foraminifera and placing it above the Awamoan Stage.

With reference to table 6, it will be noted that the correlation outside of the Oamaru district of the Hutchinsonian lead to an inflation of the stage that was not strictly intended. Fleming et al. (1969, p. 96) give the factors that lead unavoidably to Finlay & Marwick's (1940) inflation of the Hutchinsonian Stage:

(a) Correlation of Clifden Limestone with type Hutchinsonian on brachiopods (Thomson 1920; Allan 1931).

(b) Correlation of Park's (1921) bed 7 of the Clifden section with the Awamoan (the underlying beds up to bed 6 hence classified as Hutchinsonian – see (c) below) or a slightly older unit by the *Stethothyris epsilon* fauna (Finlay 1939a; Allan 1940).

(c) Close similarity of foraminifera displayed from the Hutchinsonian and Awamoan type localities – hence any age gap between the two stages was always thought to be small.

In addition, the Awamoan Stage , by correlation, held at one point two chrono-stratigraphic positions concurrently (see table 6). These anomalies in the scope of the Hutchinsonian, and in the position of the Awamoan were removed with the establishment on foraminifera of the Altonian, Clifdenian, Lillburnian and Waiauan Stages by Finlay & Marwick (1947).

Finally, Scott's (1971; 1972) biometric studies on foraminiferal lineages lead him to redefine the Altonian Stage as comprising the interval from the Otaian to the

Clifdenian. The Hutchinsonian and Awamoan Stages were subsumed into the reformulated Altonian (table 6).

1.6 Comparison of *Pachymagas tehuelcha* with New Zealand Species

The most cursory of examinations indicates immediately the striking differences between *Pachymagas tehuelcha* and New Zealand material previously assigned to that genus. Exteriorly the shells are very dissimilar – figs. 8 and 9. The shell of *P. tehuelcha* is narrower than in New Zealand specimens of the same length, with a very high beak that is suberect rather than erect, as is typical for the New Zealand "*Pachymagas*". An incipiently expressed symphytium is present in the Patagonian specimens examined (viz. F.2202d.1 and F.2202b.1, Canterbury Museum, from St. Cruz – fig. 8), the deltidial plates in the process of fusing, the plates fusing at their bases first, the locus of fusion progressing posteriorly (fig. 8). The bulk of the New Zealand species posses conjunct deltidial plates, but the younger species demonstrate possession of a symphytium (fig. 8b). *Pachymagas tehuelcha* is thicker relative both to length and to width than New Zealand material. Dorsal interiors of *P. tehuelcha* demonstrate that the moderately sized teeth rest on swollen bases, but do not seem to be grooved like the New Zealand specimens.

Interiorly there is substantially more posterior thickening in the Patagonian specimens than observed for the New Zealand specimens. The cardinal process and inner socket ridges grow together, and are seen to be fused in the holotype of *P. tehuelcha*. The hinge-trough is completely occupied and overgrown by the grossly swollen cardinal process and inner socket ridges. The specimen seen in figure 9c (left) still retains adjustor muscle scars deep in the trough, the cardinal process and inner

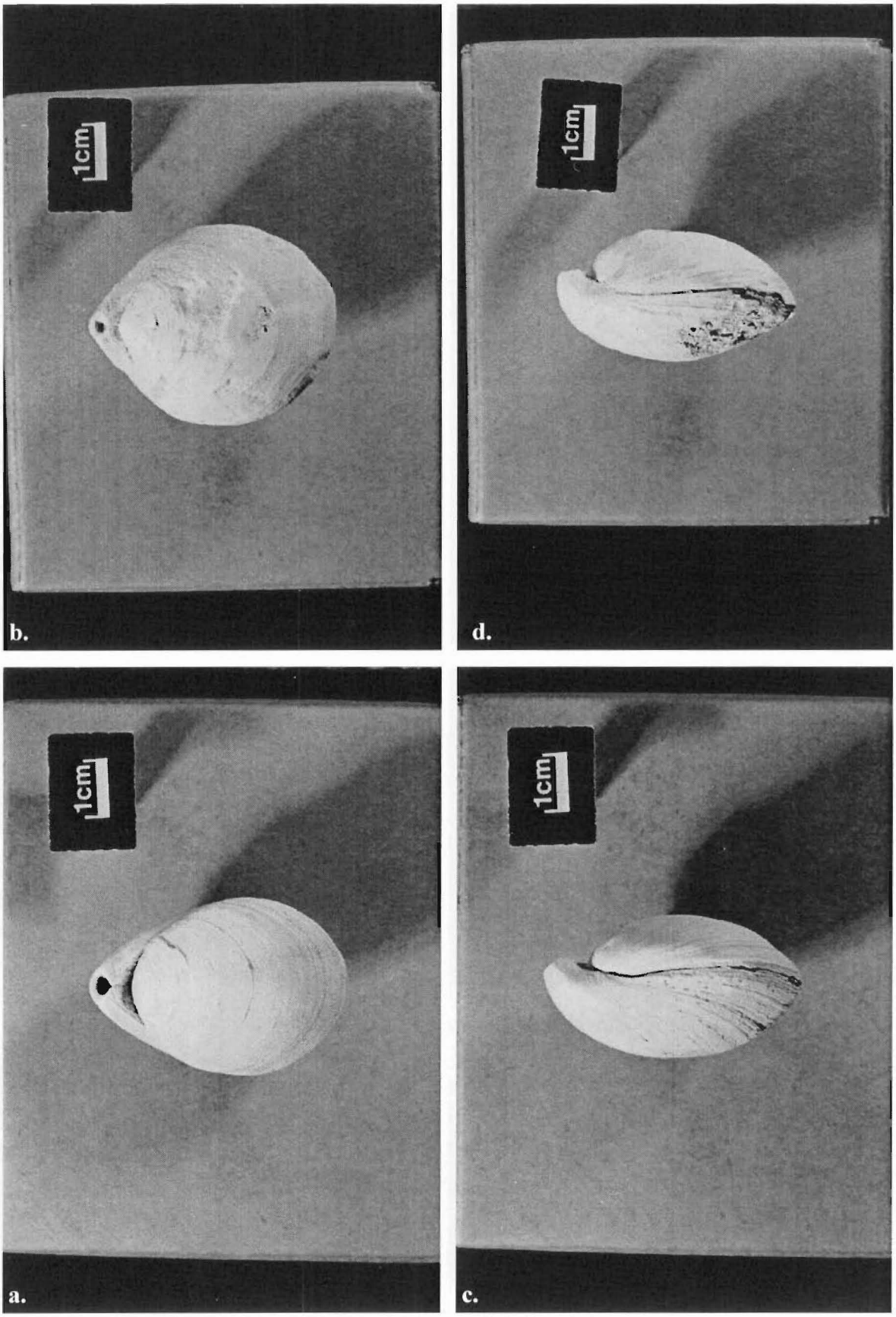


Figure 8. South American *Pachymagas tehuelcha* (**a**, **c**: F.2202b.1) and New Zealand *Waitakia bartrumi* (**b**, **d**: Allan Collection 2338).

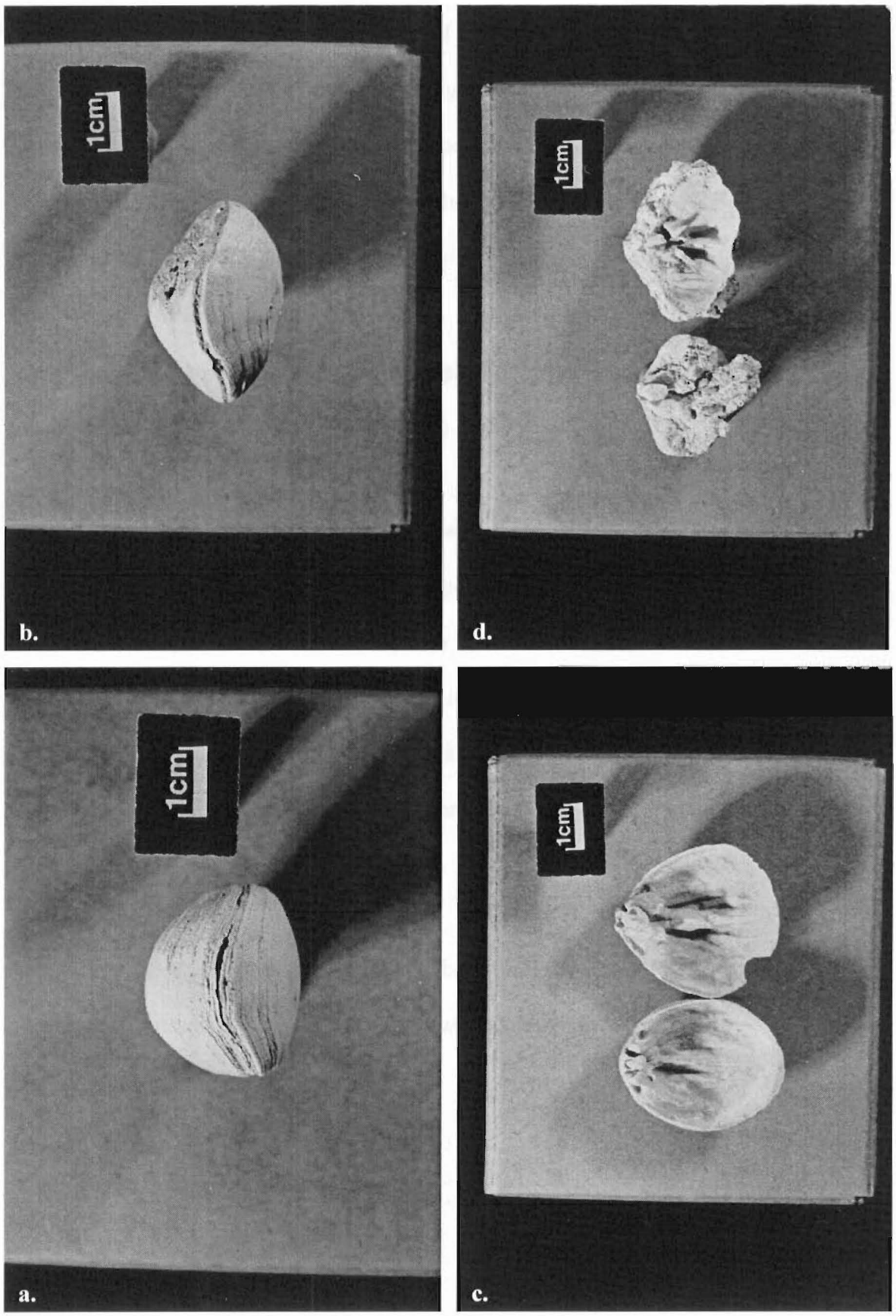


Figure 9. South American *Pachymagas tehuelcha* (**a**: F.2202b.1; **c**: F.2202b.1, F.2202d.1) and New Zealand *Waitakia bartrumi* (**b**: Allan Colln. 2338; **d**: UCM 2024, 2025).

socket ridges not being as grossly thickened as the specimen of figure 9c (right). Both specimens demonstrate the transverse ridge developed atop the cardinal process, marking the paths along which the diductor muscles ran. The median septum lacks any trace of a transverse connecting band, though the irregularities seen on the septum of specimen F.2202d.1 (fig. 9c right) *might* indicate a rather degraded attachment retained into near adulthood. The septum extends three-quarters the length of the valve in specimen F.2202d.1 (fig. 9c right), where it might be expected to be relatively short to aid in posterior weighting of the shell.

The South American genus quite possibly has its ancestry in the New Zealand genus, though they are very clearly not congeneric. As is discussed in section 1.2, it is considered likely that a species of *Waiparia* Thomson (sister genus of "*Pachymagas*") was transported via the circum-antarctic current to occur in strata of the Antarctic Peninsula. It is quite feasible that representatives of the genus travelled further, either from New Zealand or the Antarctic, and made their way into the Miocene waters of South America.

The New Zealand species should be withdrawn from *Pachymagas*, as such they are here placed in a new genus – *Waitakia*, defined on page 47.

Chapter Two:

'Historic Works'

2.0 History of Systematic Description

While authors such as F. W. Hutton and A. R. Andrew were the first to describe species that have been placed in the genera of this study, their contributions to investigation and further development of the genera are minor compared to those of J. A. Thomson and R. S. Allan. For this reason the works of the two primary authors, Thomson and Allan, are the subject of this chapter, while initial identifications of earlier authors are recognised in the synonymies of Chapter Three.

2.1 J. A. Thomson

J. A. Thomson (Thomson 1915) first referred New Zealand brachiopods to the South American genus *Pachymagas* von Ihering when he figured interiors for the species *Pachymagas parki* (previously *Magellania parki* Hutton, 1905), and his new species *P. huttoni*. Thomson's figure is notable in being the first to demonstrate the interior characteristics of the New Zealand *Pachymagas*. Figured interiors for this genus are few amongst the relevant works of Thomson, his photographic plates not as clearly demonstrating the nature of the cardinalia. For these reasons Thomson's figure is reproduced here as figure 10, with the added note that, as Allan (1937a, p. 121) states, fig. 2a (fig. 10a as reproduced here) of Thomson's original figure is not in fact *P. parki*. Thomson later corrected this mistake (Thomson 1927, p. 89), identifying the figured specimen as *P. cottoni*, though it is here

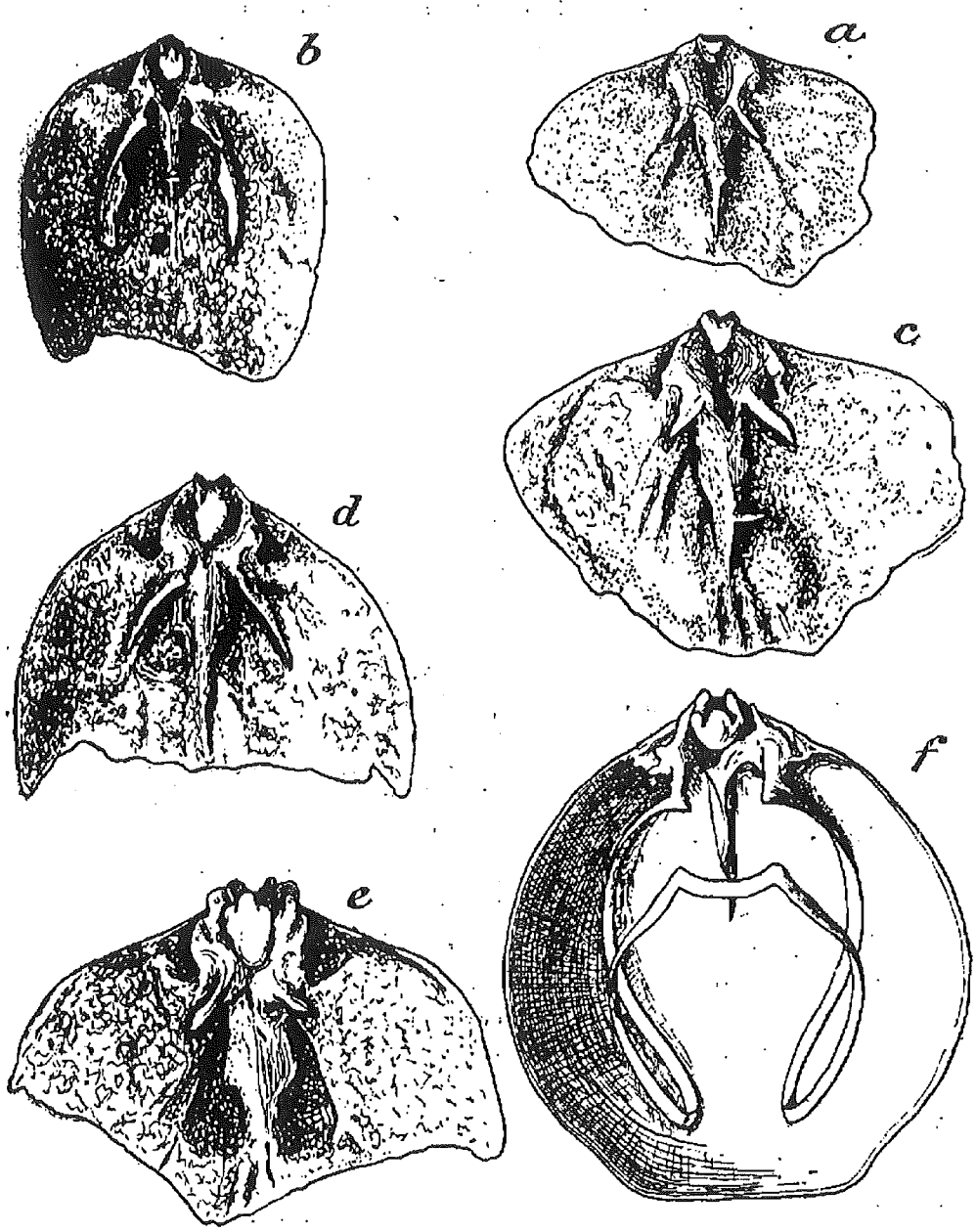


Figure 10. Interiors of dorsal valves of New Zealand species of *Pachymagas* and *Neothyris*, coarsely demonstrating the evolution of the cardinal process. **a**. *P. cottoni* Thomson, Kakanui greensands. **b**. *P. parki* (Hutton), Hutchinson's Quarry greensands. **c**. *P. huttoni* Thomson, Wharekuri greensands. **d**. *N. ovalis* (Hutton), Shakespeare Cliff. **e**. *N. ovalis* (Hutton), Castlecliff. **f**. *N. lenticularis* (Deshayes). Enlarged. (From Thomson 1915, 1927)

considered to be a different species entirely, the figure representing *Waitakia alldayi* n. sp. (section 3.3).

It is worth noting here that, after a visit to the United States and examination of Patagonian Tertiary brachiopods from various collections, Allan (1949) concluded that the New Zealand species were not closely related to the South American genus. After this date he referred to the New Zealand genus as "*Pachymagas*" (Allan 1957, 1960). However, this convention is not used in *this* chapter, as both Patagonian and New Zealand species are discussed, and also because in some of the works discussed, it is not always easy to ascertain whether the *Pachymagas* mentioned are exclusively the New Zealand species. While the New Zealand "*Pachymagas*" is placed in the new genus *Waitakia* in this study, discussion of the works of Thomson and Allan in this chapter require that the term *Pachymagas* be retained throughout this chapter for reasons of clarity.

Throughout his works Thomson discriminates relatively between "advanced" and "primitive" states of development of characters, particularly with regard to the cardinal process, and also folding. The paragraph below demonstrates what Thomson meant by these terms, and also outlines the evolution of the cardinal process in the lineage (which is somewhat coarsely illustrated in fig. 10):

"In New Zealand older Tertiary examples of *Pachymagas* it [the cardinal process] is always fairly simple, but differs greatly in size and in height. In its most primitive form it is very short, being confined to the posterior part of the hinge-trough, and is also very low, in shape being a pyramid with an edge facing forwards and a hollowed side behind. In more advanced types the process gains both in length, occupying more and more of the hinge-trough, and in height, projecting above the socket-ridges, while the hollow behind is now confined to its base, and is bounded by two lateral ridges. In the most advanced types met with in New Zealand species of *Pachymagas* there is a slight posterior median ridge in the upper part of the process,

and this ridge becomes still more accentuated in the Patagonian late Tertiary species, including *P. tehuelcha*, the genotype, and in the most primitive species of *Neothyris* of New Zealand, while at the same time the process gains both in length and height. Finally, in *N. lenticularis* the process is so large that it fills the whole of the hinge-trough, and almost hides the bifurcation of the septum; the posterior median ridge is strongly marked, while the two lateral ridges bounding the hollow facet at the bottom of the posterior part of the process are greatly developed, and incurved so that they nearly meet to form a tube." (Thomson 1915, p. 395-396)

The cardinal process can therefore be considered a peramorphic character in *Pachymagas*; hence an "advanced" cardinal process might alternatively be described as "peramorphic". However, the terms "advanced" and "primitive" are retained because they can be used outside of an heterochronic framework, and are conceptually simpler terms.

Thomson (1915) also made the observation that, as the hinge characters of *Pachymagas tehuelcha* resemble those of *Neothyris lenticularis*, it was a certainty that *N. lenticularis* had an ancestor that possessed Pachymagoid hinge-characters, with a terebratelliform loop; the New Zealand *Pachymagas* of course fitting this bill. Thomson suggested a "magaselliform" ancestor for *Pachymagas* itself, developed through anterior enlargement of the hinge-trough of *Magadina*. He later (1927) advocated *Jaffaia* as the possible ancestor, but stipulated that juvenile loops of *Pachymagas* would have to be examined to establish that relationship.

In Thomson's (1917) paper concerned with diastrophic correlation, he described (though did not figure) the species *Pachymagas abnormis* and used its occurrence in the mudstone overlying the Takaka Limestone of the Aorere Valley to suggest an "Upper Oamaruian" age for the limestone. Thomson cited the occurrence of both *Pachymagas abnormis* in the overlying mudstones, and *Neothyris novara* in the Takaka Limestone as evidence that the limestone was younger than the

"Ototaran", and that the Takaka Limestone was consequently not of the same age as the Ototara Limestone. This decision was based on correlation with the "Hutchinsonian" Mount Brown middle and uppermost limestone of the Weka Pass district, North Canterbury. There, both *Neothyris novara* and *Pachymagas abnormis* are found in association with brachiopod faunas Thomson considered "Hutchinsonian".

Though Thomson considered *Pachymagas abnormis* as strictly "Hutchinsonian", specimens (see section 3.0) from Otago demonstrate that the species occurs in the Waitakian, and thus ranges from the Waitakian through to the Altonian. Allan (1960) also stated that Thomson's record of *Neothyris novara* from the uppermost limestone (or "E" limestone, of Thomson's 1920 terminology) of Mount Brown was based on a misidentification. Allan further stated that this species Thomson placed in the genus *Neothyris novara* is widely separated in time from the Recent genotype, and the Pliocene ancestors of this Recent species. Allan (1960, p. 240) informed that the species "...may be referred to as '*Neothyris*' *novara* (von Ihering). It is probably related to '*Pachymagas*' *huttoni* Thomson." *Neothyris* (?) *novara* is considered unrelated to "*Pachymagas* huttoni" (*Waitakia marshalli*) in this study.

Two new, unillustrated, species were established with Thomson's (1918a) brachiopod identifications in the appendix to Park's work on the geology of the Oamaru district, viz. *P. trelissickensis* and *P. ellipticus*. Accompanying these are two species previously described under *Magellania*, and which Thomson here placed in *Pachymagas* – *P. triangularis* and *P. marshalli*. However, Thomson immediately synonymised *P. marshalli* with *P. parki*, noting that:

"*P. marshalli*, although very different in shape from the holotype of *P. parki*, seems linked up to it by insensible gradations, and has here been treated as a synonym. *P. parki*, as here conceived, is therefore a polymorphic species, all the members of which are of a similar size, and possess mesothyrid foramens of moderate size." (Thomson 1918a, p. 118).

At this date, then, Thomson's conception of *P. parki* was an inclusive one, including as it did various distinguishable forms. However, Thomson's description of *P. parki* as a polymorphic species is somewhat at variance with the statement that *P. marshalli* seems linked up to *parki* through insensible gradations, as common conception of polymorphism stipulates the occurrence of discontinuous rather than continuous phenotypes, within a single population (e.g. Mayr 1970).

The geographic and time ranges of *P. abnormis* are extended in Thomson's (1918b) paper on the age of the Waikouaiti Sandstone. He records the occurrence of *P. abnormis* from the Waikouaiti Sandstone of the Dunedin district, the "Hutchinsonian" greensands and "Awamoan" mudstones of All Day Bay, and from a higher horizon (the "Rhizothyris-Pachymagas bed" of Fleming 1963) than that of the holotype, at Weka Pass.

It is possible that this additional record from the "Rhizothyris–Pachymagas bed" (Fleming 1963) of Weka Pass is due to a misidentification by Thomson of the closely related *W. intermedia* (section 3.1), though its occurrence at this horizon cannot be unequivocally ruled out. Again, Thomson (1918b) concludes that the presence of *P. abnormis* indicates an "Upper Oamaruian" rather than an "Ototaran" age for the Waikouaiti Sandstone.

Doubts about the generic position of *P. abnormis* were first raised by Thomson in the above paper:

"Mr. S. S. Buckman, of Thame, England, has suggested that *Pachymagas abnormis* should not be referred to *Pachymagas*, but should be made the type of a new genus on account of its beak characters, and if this course it followed it would be possible to differentiate a number of species within the somewhat variable series I have referred to *P. abnormis*. The specimens from the "Awamoan" mudstones of All Day Bay and from the Waikouaiti Sandstone would, however, still have to be retained in the same species." (Thomson 1918b, p. 197)

Thomson (1920) later obliged, establishing the new genus *Waiparia*.

The brachiopod identifications of Gudex's study on the Tertiary beds of the Pareora district were made by J. A. Thomson (Thomson 1918c). The species Thomson identified were *P. parki*, *P. ellipticus*, and *P. huttoni*, all recorded from the Otaio limestone, with *parki* additionally recorded from the overlying blue clay and sandstone. The co-occurrence of these three species, which Thomson later (Thomson 1926) considered characteristic elements in faunas of different ages (*P. parki* an element of "Hutchinsonian" faunas; *P. ellipticus* and *P. huttoni* elements of "Ototaran" faunas), is probably due to a conception of *P. parki* that, at that time, was too inclusive.

The majority of New Zealand species of *Pachymagas* were first described in Thomson's (1920) paper "The Notocene Geology of the Middle Waipara and Weka Pass District, North Canterbury, New Zealand". Most remarkable is the fact that the bulk of these species were described from a single horizon, viz. "Foot of dip-slope, main Mount Brown limestone, Weka Pass". This horizon has been informally called the "Rhizothyris-Pachymagas bed" by Fleming (1963). From this horizon, at just one

locality were recorded the following brachiopods: *Bouchardia minima*, *Magadina browni*, *Rhizothyris amygdala*, *R. crassa*, *R. curta*, *R. elliptica*, *R. elongata*, *R. fortis*, *R. obesa*, *R. ovata*, *R. pirum*, *R. rhizoida*, *R. scutum*, *Pachymagas bartrumi*, *P. coxi*, *P. haasti*, *P. hectori*, *P. mckayi*, *P. morgani*, *P. parki*, *P. speighti*, and *Terebratulina suessi*. Of these species, all but *B. minima*, *M. browni*, *P. parki*, *R. rhizoida, and T. suessi* were new species and, of the new species, all but *R. scutum*, *R. elongata*, *R. amygdala*, *P. haasti*, and *P. hectori* have the "Rhizothyris-Pachymagas bed" as their type locality. Bowen and Campbell's (1973) restudy of *Rhizothyris* showed that all nine of the species from the Main Mt Brown Limestone could be regarded as synonyms, and were all classed as *Rhizothyris rhizoida.*

It is both interesting and alarming to note that many of these species are established or referred on the basis of one or at most a few individual specimens, some even poorly preserved (e.g. the holotype of *Pachymagas marshalli*). Most new species are figured without interiors, nor are the interior characteristics described, though this is somewhat understandable due to hardness of the enclosing matrix, and rarity of specimens available for potentially destructive excavation. Some species cannot even be referred definitively to a particular genus due to an ignorance of the interior characteristics – for example, Thomson (1920) stated that *P. andrewi* could conceivably belong to *Neothyris* rather than *Pachymagas*, the specifics of the loop being unknown (examination of the holotype in the National Museum of New Zealand, which has been partially excavated from the ventral side, demonstrates the specimen possibly possesses a transverse connecting band; additional excavated specimens also suggest the loop was trabecular – see section 3.11). The effective lack of data precludes any comment on intraspecific variation for some species.

A very illuminating paragraph on the occurrence and characteristics of the Rhizothyrid fauna of the Mount Brown limestone follows, relevant to this study because it demonstrates the systematic thinking of Thomson, the profusion of species names for *Rhizothyris* paralleling those of *Pachymagas*:

"Specimens of *Rhizothyris* are extremely abundant in the main Mount Brown limestone (D), and less so in the uppermost limestone (E). They present a great variety of form, the extremes being so different that it is impossible to imagine that they had not been differentiated into separate true-breeding races, although there are so many intermediates that it is obvious that the evolution had taken place only a short time previously or was still in progress. Similar polymorphism is displayed by the specimens from Hutchinson's Quarry, Oamaru, the Maerewhenua greensands, and the Curiosity Shop. As the forms are not exactly the same in these localities, and as a stratigraphical value may be found to attach itself to certain forms, it is desirable to create species for all the distinctive types." (Thomson 1920, p. 370)

Likewise, for *Pachymagas* Thomson states:

"As is the case of *Rhizothyris*, specimens of *Pachymagas* are abundant in the main Mount Brown limestone (D), and they present an even greater variety of characters. Similar series occur in the Hutchinsonian greensands of Hutchinson's Quarry, Deborah, Kakanui, and other localities near Oamaru, while there is a different but even more varied assemblage in the Curiosity Shop greensands." (Thomson 1920, p. 374)

Notably, Thomson sees the occurrence of intermediates between all of his species forms of the "D" limestone as evidence of the recent or ongoing evolutionary process, rather than merely an expression of intrapopulational/intraspecific variability. On appearances, the admission of variability among the species of the limestone seems a far simpler explanation for the variety of form.

In Thomson's (1920) efforts to treat *Pachymagas* on evolutionary lines, he divided the genus into a number of, ideally, phylogenetic series. He noted that the evolutionary process in *Pachymagas*, deduced from the ontogeny of the descendent

genus *Neothyris*, is "from depressed to convex, from large to small foramen, and from suberect to erect and produced beak." (Thomson 1920, p. 374). Hence, in an heterochronic framework, the lineage is undergoing "dissociated heterochrony" (i.e. the foraminal development in the lineage is paedomorphic while, as discussed previously, the development of the cardinal process in the lineage is peramorphic), or to put it more traditionally, "mosaic evolution". The shape, folding, and cardinalia could all be treated on evolutionary lines, according to Thomson.

The phylogenetic series arranged by Thomson (1920) were:

Pachymagas parki **Series** "...arranged according to shape in a series from suborbicular to narrowly ovate, but do not all form a strictly phylogenetic series, owing to variations in the amount of folding." (Thomson 1920, p. 374)

P. marshalli	*P. cottoni*	*P. bartrumi*	*P. speighti*
P.clarkei	*P. haasti*	*P. hectori*	*P. parki*
P. mckayi	*P. morgani*	*P. trelissickensis*	*P.coxi*

"probably" including:

P. tehuelcha (Patagonian) *P. gigantea* (Patagonian)
P. antarctica (Antarctic)

Pachymagas huttoni **Series**

P. huttoni	*P. triangularis*	*P. venter* (Patagonian)

***Pachymagas ellipticus* Series** "...perhaps generically distinct..." (Thomson 1920, p. 374)

P. ellipticus

Thomson (1920) at this time established the genus *Waiparia*, placing *P. abnormis* and *W. intermedia* within. He stated that the "genus may be considered as springing from the same stock as *Pachymagas*, but lagging behind in foraminal evolution. It possibly gave rise directly to *Pachymagas* of the type of *P. ellipticus*, which possesses a foramen which is submesothyrid but almost mesothyrid." (Thomson 1920, p. 380). As previously stated, Thomson (1927) later placed *P. ellipticus* in *Waiparia*, also noting that *P. ellipticus* occurs in an earlier geological horizon than do *W. abnormis* and *intermedia*. In this study it is thought that *W. abnormis* might range as far back as Whaingaroan, and is certainly found in the Waitakian (section 3.0).

Thomson (1926) includes discussion on *Pachymagas* in his brachiopod evidence for the age of the Waitaki Limestone, where he notes that his previous conceptions of species of the genera *Rhizothyris* and *Pachymagas* "admitted considerable variation and brought together dissimilar forms which it is better to attempt to distinguish specifically even if they are apparently united by intermediates." (Thomson 1926, p. 149). This stance explains the great number of species of these genera found in Thomson's (1920) paper on the Middle Waipara and Weka Pass. Thomson's insistence on brushing aside the occurrence of intermediates between his species forms, or their explanation by some rather fantastic evolutionary gymnastics (i.e. intermediates in the "Rhizothyris-Pachymagas bed" are considered to owe their resemblance, to those species to which they are intermediate, to some

'middle path of evolution'), appears to be due to his ardent desire that they have every chance of finding some stratigraphic value.

Thomson (1926) stated that the brachiopods crowding the "Hutchinsonian" greensands of the Oamaru coastal district were almost exclusively species belonging to the *Pachymagas parki* series. He noted that the mean around which variation took place differed between these different localities. Thomson took this to indicate that hybridism was an important factor in producing the shape diversity. However, if one was to assume that at each locality there was but one variable species of *Pachymagas*, rather than a whole series of complexly related species, variation about a slightly different mean would not be unexpected given that separate populations would have existed at each locality.

Thomson (1926) speculated that the Hutchinson's Quarry greensands might represent a compressed deposit, as the difference in fauna suggested a difference in horizon, one of younger age due to the 'advanced state of evolution' of the folding and cardinal process of the *Pachymagas* there. Noting that the coeval existence of species at different relative stages of evolution was not unheard of, Thomson cautioned that the two faunules should not unequivocally be considered of different ages until found in sequence.

Pachymagas cf. *ellipticus* and *Pachymagas* cf. *huttoni* were part of the fauna Thomson (1926) included in his so-called *Liothyrella landonensis* fauna. Although *Pachymagas ellipticus* is an often present and important component of the fauna, the inclusion of *P. huttoni* in the fauna is questionable. This important fauna has come to

be considered indicative of the Duntroonian Stage (Allan 1938b; MacKinnon et al. 1993).

In the book "Brachiopod Morphology and Genera (Recent and Tertiary)" (Thomson 1927) the holotype of *Pachymagas*, the South American species *P tehuelcha*, is figured. Comparison of this figure (a reproduction of von Ihering's original 1903 illustration) with those Thomson gives for the New Zealand species in the publication indicate startlingly obvious and marked differences between the Patagonian and New Zealand forms. A comparison of the genotype and New Zealand species is covered in section 1.6.

Thomson (1927) again attempts to demonstrate phylogenetic relationships by arranging Patagonian, Antarctic, and New Zealand species in phylogenetic series:

***Pachymagas tehuelcha* series**

Pachymagas antarcticus Buckmann

Magellania parki Hutton "and numerous other species"

Terebratella parki Ihering

Terebratella gigantea Ortmann

***Pachymagas venter* series**

Waldheimia triangularis Hutton

Pachymagas huttoni Thomson "and related undescribed species"

Terebratella venter piramidesia Ihering

***Pachymagas andrewi* series**

Pachymagas andrewi

"The New Zealand species of the typical series are geologically older than those of Patagonia, and have less-developed cardinal processes (see fig. 29). In the New Zealand stock, when the cardinal process has developed as far as those of the Patagonian species, which occurs in the uppermost Miocene and the Pliocene, the loop has also developed to the magellaniform stage, necessitating reference to the genus *Neothyris*. This development of the loop does not appear to have taken place in the American region, where *Neothyris* is absent, unless in the species *Terebratula fontainei* d'Orbigny. The American species of *Pachymagas* have lagged behind in loop-development while the development of the cardinal process has gone on. It hardly seems necessary to erect a new genus for the more primitive New Zealand species, since they are obviously of the same stock." (Thomson 1927, p. 287-288)

From this excerpt it is seen that Thomson still did not recognise a generic difference between the New Zealand and South American species, despite noting the significant differences in relative degrees of development of the loop and cardinalia.

2.1.1 Selected Bibliography for J. A. Thomson

PARK, J., 1918, The geology of the Oamaru district, North Otago (eastern Otago division). *New Zealand Department of Mines, Geological Survey Branch, Bulletin n.s. 20*, p. viii + 1-124, 3 maps, 3 sections, pl. I-XII

THOMSON, J. A., 1908, Fossils from Kakanui. *Transactions and Proceedings of the New Zealand Institute 40*, p. 98-103, pl. XIV

THOMSON, J. A., 1915, Brachiopod genera : the position of shells with magaselliform loops, and of shells with bouchardiform beak characters. *Transactions and Proceedings of the New Zealand Institute 47*, p. 302-403

THOMSON, J. A., 1916, On the stage names applicable to the divisions of the Tertiary in New Zealand. *Transactions and Proceedings of the New Zealand Institute 48*, p. 28-40

THOMSON, J. A., 1917, Diastrophic and other considerations in classification and correlation, and the existence of minor diastrophic districts in the Notocene. *Transactions and Proceedings of the New Zealand Institute 49*, p. 397-413

THOMSON, J. A., 1918a, Appendix 3 : Brachiopoda, p. 117-119 *in* Park, J., 1918, q.v.

THOMSON, J. A., 1918b, On the age of the Waikouaiti Sandstone. *Transactions and Proceedings of the New Zealand Institute 50*, p. 196-197

THOMSON, J. A., 1918c, Brachiopod identifications *in* Gudex, M. C., 1918, The succession of Tertiary beds in the Pareora district, South Canterbury. *Transactions and Proceedings of the New Zealand Institute 50*, p. 244-262, pl. XVI-XVII

THOMSON, J. A., 1920, The Notocene geology of the Middle Waipara and Weka Pass district, North Canterbury, New Zealand. *Transactions and Proceedings of the New Zealand Institute 52*, p. 322-415, pl. XVI-XXVII

THOMSON, J. A., 1926, Marine phosphatic horizons in the Tertiary limestones and greensands of South Canterbury and North Otago, and brachiopod evidence as to their age. *New Zealand Journal of Science and Technology 8 (3)*, p. 143-160

THOMSON, J. A., 1927, Brachiopod Morphology and Genera (Recent and Tertiary). New Zealand Board of Science and Art, Manual No. 17. Government Printer, Wellington, p. vi + 1-338, pl. 1-2

2.2 R. S. Allan

Allan's first work of relevance with respect to this discussion of *Pachymagas* and *Waiparia* is his study on the Waihao Basin (Allan 1927), the brachiopod identifications being made by J. A. Thomson. Identifying *Pachymagas ellipticus* from the Waihao limestone, Thomson commented that the species was really a series of species, noting that the range of variation paralleled that for other localities (Landon Creek, Papakaio, Duntroon) where *ellipticus* is found. He notably made no effort to differentiate the series into species, and no authors have since.

It is highly significant that Thomson earlier sought to differentiate species of *Pachymagas* finely, but by this stage had to resort to placing them in more inclusive series, and referred the *series* as occurring, rather than specific species of it. The conclusion perhaps to be made that Thomson himself latterly found it difficult to place some occurrences within species he had created (c.f. Thomson 1920 when he sought to finely divide them).

A single specimen from Clifden Quarry, Southland, was the first species Allan (1931) himself placed in *Pachymagas*, naming it *P. turneri.* In his later paper on Tertiary brachiopods of the Chatham Islands (Allan 1932), four species are placed in the genus (on the advice of J. A. Thomson), despite the fact that all of them possessed rectimarginate commissures, and having no knowledge of the loop morphology (Allan noting that *Pachymagas* differs from *Neothyris* only in having attained a magellaniform (teloform) stage of development). He stated that the development of commissural folding had either lagged behind the species of mainland New Zealand, or was a primitive character, depending on whether the tuffs they were collected from were "Hutchinsonian" or "pre-Hutchinsonian", respectively. Allan later placed these three species (and suggested also that they possibly represented a single variable species) in *Neothyris* noting that the Opoitian foraminifera H. J. Finlay had identified from the tuffs (Allan 1960, p. 249) pointed to *Neothyris* rather than *Pachymagas*.

In his revision of the New Zealand System and Stage names, Allan (1933) notes, Thomson (1926, p. 151) having given the evidence, that the Hutchinson's Quarry greensands (from which the "Hutchinsonian" Stage takes its name) differ in age from the other greensand localities Thomson correlated (e.g. Thomson 1920) with Hutchinson's Quarry. This being the case, a new basis for the Stage needed to be

defined. Allan, as an interim measure, suggested the "Hutchinsonian" be defined as "...the period of time during which the *Pachymagas parki* series of brachiopods were the characteristic fauna." (Allan 1933, p. 89). Apparently, the *Pachymagas parki* series is that as arranged by Thomson (1920), and as recorded in his paper on marine phosphatic horizons (Thomson 1926). As such, the series includes *P. haasti* and *P. hectori* recorded (e.g. Thomson 1920, 1926) from the Oamaru coastal greensands. Allan noted that four distinct faunal divisions of the "Hutchinsonian" could be made, the *Pachymagas parki* assemblage and the *Pachymagas hectori* assemblage being among them. The brachiopod fauna of the Waitakian Stage, newly defined by Allan (1933), consisted of species of the *Pachymagas huttoni* series (again, apparently as established by Thomson 1920), though Thomson (1926, p. 155) noted species intermediate between the *parki* and *huttoni* series.

Allan (1937b) termed the orange-coloured *Magadina* sands below the "Rhizothyris-Pachymagas" bed of Fleming (1963) the "Magadina Bed", recording a large brachiopod, *Pachymagas bensoni*, from there. Figure 11 denotes the stratigraphic position of this horizon, along with the "Rhizothyris-Pachymagas bed" and the "Mount Donald horizon" (defined below).

Allan applied the term "Mount Donald horizon" to the discontinuous fossiliferous horizon of "Hutchinsonian" age at the base of the main Mount Brown limestone between Mt. Donald and Weka Pass, and extending perhaps a metre into the calcareous sands below (Fig. 11). Wilson (1963, fig. 15) tentatively figured this horizon some distance below its true position, which as Allan states is at the base of the main Mount Brown limestone. The horizon was found to be located as Allan described it during fieldwork, and not as figured by Wilson (1963); figure 11

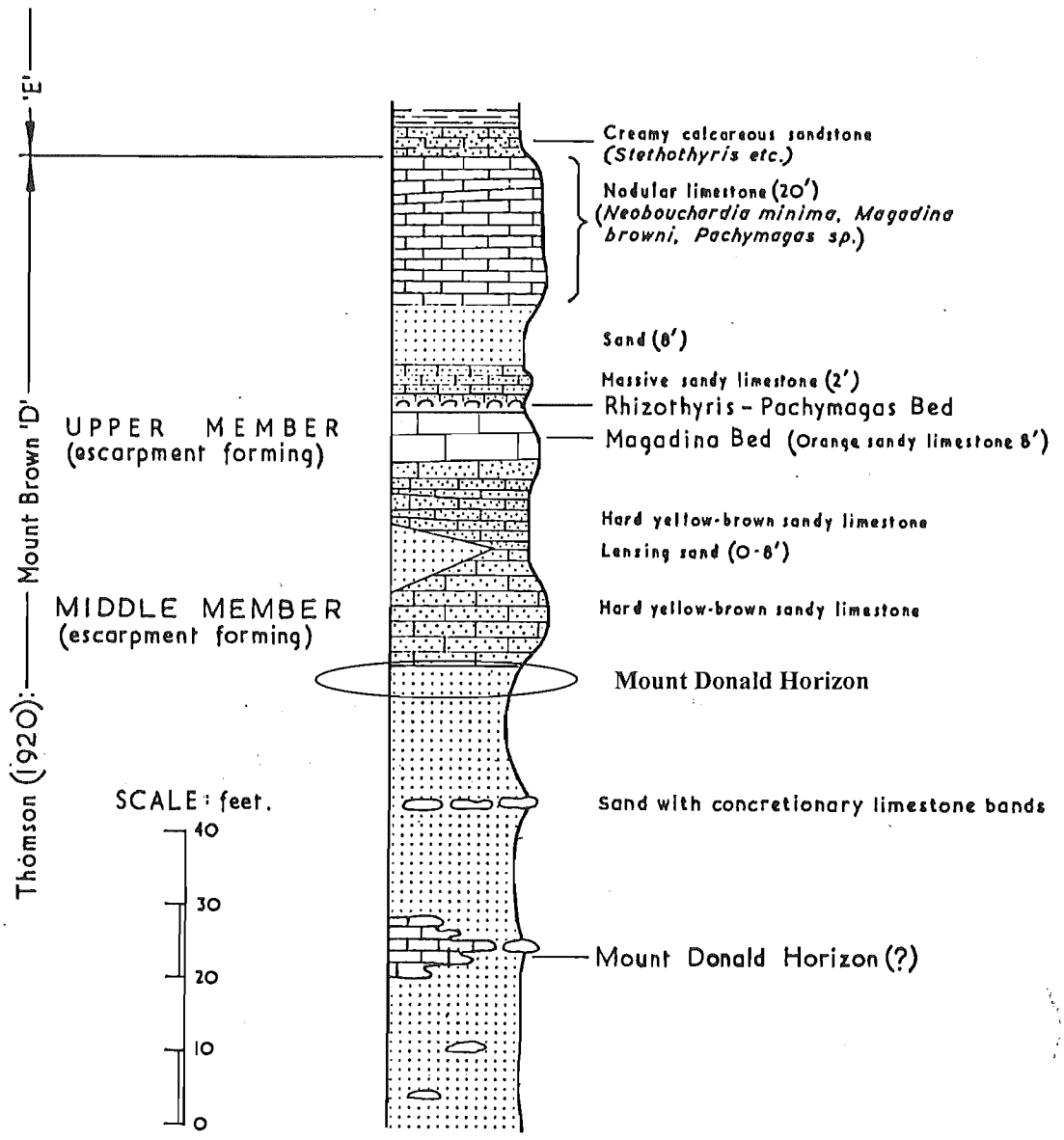


Figure 11. Column illustrating members and macrofossil horizons in the main Mount Brown limestone of Weka Pass. Note that the Mount Donald horizon as defined by Allan is located at the base of the main Mount Brown limestone in the figure, and is noted in bold-faced type. It is *not* the horizon as demonstrated at the bottom of the figure. (Modified from Wilson, 1963)

demonstrates its true stratigraphic position. Allan equated the Mount Donald horizon with that horizon described by Park (1905, p. 540), and that from which *Waiparia abnormis* and *Pachymagas cottoni* were described by Thomson (1920). The brachiopods listed by Allan (1937c) include *Magadina browni*, *Neothyris* (?) c.f. *anceps*, *Pachymagas cottoni*, *P. forbesi*, *P. haasti*, *P. hoodi*, *P. morgani*, *P. turneri*, *Rhizothyris elliptica*, *Waiparia abnormis*, *Waiparia intermedia*; *P. forbesi* and *P. hoodi* were new species that were duly described and figured by Allan (1937c, p. 134-135, pl. XVIII). Again, this list does appear to include a large number of congeneric species occurring at one horizon, with subtle shape differences once more distinguishing some species – e.g. *Pachymagas hoodi* is "...related to *P. cottoni* Thomson from the same horizon but differs in being more ovate, has more convex sides and a more curved hinge-line." (Allan 1937c, p. 135). Whether forms such as these are related through speciation, or variation, is open to question, the results of this study suggesting that variation is the better answer.

Intermediates are again a feature of the fauna described by Allan (1937d) from the "Hutchinsonian" Forest Hill Limestone sequence of Southland, along with large numbers of congeneric species occurring in individual horizons. Allan (1937d) adds to the growing systematic list of *Pachymagas* by erecting four further species, viz. *P. finlayi*, *P. mcdowalli* (type locality Clifden), *P. ulrichi*, and *P.* (?) *uttleyi* (though he notes of this species that it may be congeneric with *Neothyris* (?) *anceps* Thomson). The interior characteristics of the four new species were not determined by Allan.

Allan comments upon the difficulty of species-making at most such "Hutchinsonian" localities, noting that the *Pachymagas* in the middle limestone horizon from Centre Bush and Limehills (the quarries at each locality from where

Allan described the sequence) display an "almost bewildering variety of form"; even more so than *Rhizothyris*. He states: "Seven species, three of which are new, have been recognised, but many specimens are intermediate in either a single character, or in the sum total of their characters; and imperfect material suggests that renewed collecting will yield still further new species." (Allan 1937d, p. 143).

Brachiopod identifications in Speight's bulletin on the Mount Somers district were made by Allan (Allan 1938a). In an appendix to the bulletin, Allan establishes the Duntroonian Stage for strata containing the widespread (throughout North Otago and Canterbury) *Liothyrella landonensis* fauna (of Thomson 1926), placing the Stage between the "Ototaran" and the Waitakian, dismissing Thomson's "Upper Ototaran" age for the fauna (Allan 1938b).

The highly distinctive brachiopod from Balfour Quarry in Southland, which Allan named *Pachymagas balfourensis* (Allan 1940) is inappropriately referred to the genus. As Allan suspected, cleaned interiors (fig. 74) reveal that the species does not have a transverse connecting band, the loop being teloform; further, the cardinalia is found to be very dissimilar to New Zealand species previously referred to *Pachymagas*. Allan compared *P. balfourensis* with the Patagonian form *P. venter*, noting the exterior and interior similarities and, following Thomson's (1927, p. 287) suggestion that the *P. venter* series might be generically distinct, agreed that this might be true of this form also. Other material found suggested to Allan the presence of *Waiparia elliptica*, implying to Allan a possible Duntroonian age for the associated *P. balfourensis*. The present study shows that this material represents instead *Waitakia marshalli* (section 3.9). Allan (1960, p. 240), noting its association with

Athlopecten at Balfour Quarry, placed *P. balfourensis* in the Waitakian Stage; this is in accord with the known range of *W. marshalli* (section 3.9).

Allan's (1949) trip to the United States and his examination of South American species there has already been commented upon. Among the conclusions drawn by him were that *Pachymagas* is an endemic South American genus, not closely related to the New Zealand species. A comparison of the genotype with New Zealand species is covered in section 1.6.

In an appendix to Gage's bulletin on the Waitaki Subdivision, Allan (1957) summarised the brachiopod fauna, giving supplementary notes. He remarked that the fauna of the lower Gee Greensand of the Oamaru coastal district (excluding Hutchinson's Quarry), shown on foraminiferal evidence to be of Otaian age by H. J. Finlay (Allan 1957, p. 106), consists of polymorphic swarms of large brachiopods which Thomson placed in *Pachymagas*. He remarks "The variability of the assemblages poses a nice problem in speciation which is not yet solved." (Allan 1957, p. 106). Of passing note, Allan records a new species of *Pachymagas* as occurring in the "Awamoan" "Turitella" shell bed at Old Rifle Butts. This bed was examined during the course of this study, with no brachiopods referable to the New Zealand genus being found.

Allan (1960) summarises the occurrence of species and faunas already mentioned, placing them in the amended stratigraphic framework developed by Finlay (1939-1947) and Finlay & Marwick (1940, 1947). Commenting on the fauna of the "*Rhizothyris* bed" (Rhizothyris-Pachymagas bed of Fleming 1963) Allan said:

"The writer is not satisfied that Thomson's philosophy of speciation in '*Pachymagas*' and *Rhizothyris* was sound; and is inclined to suspect that in each genus these polymorphic swarms represent populations of freely inter-breeding members of a single species. Work is in progress on a statistical analysis of the Rhizothyrids of this bed to test this point of view." (Allan 1960, p. 245).

Allan never published such an analysis, though Bowen and Campbell (1973) did. Allan was to later inform C. A. Fleming that:

"Modern views on speciation would suggest that the polymorphism noted by Thomson could be better explained by the theory that at particular horizons in the main Mount Brown limestone we are dealing with variants in what are freely interbreeding communities of a single species." (Fleming 1963, p. 47).

The relationship between the two Neothyrids *Neothyris* (?) *anceps* and *N. iheringi*, and *Pachymagas* was also queried by Allan (1960, p. 248) who concluded that it was not readily apparent whether or not they were in fact offshoots of *Pachymagas*.

2.2.1 Selected Bibliography for R. S. Allan

ALLAN, R. S., 1927, The geology and paleontology of the lower Waihao Basin, South Canterbury, New Zealand. *Transactions and Proceedings of the New Zealand Institute 57*, p. 265-309

ALLAN, R. S., 1931, Description of Tertiary Brachiopoda from New Zealand, Part I. *Transactions and Proceedings of the New Zealand Institute 62 (2)*, p. 156-160, pl. 20-22

ALLAN, R. S., 1932, Tertiary Brachiopoda from the Chatham Islands, New Zealand. *Transactions and Proceedings of the New Zealand Institute 63 (1)*, p. 11-23, pl. 4-6

ALLAN, R. S., 1933, On the system and stage names applied to subdivisions of the Tertiary strata in New Zealand. *Transactions and Proceedings of the New Zealand Institute 63 (2)*, p. 81-108

ALLAN, R. S., 1937a, Type Brachiopoda in the Canterbury Museum. *Records of the Canterbury Museum 4 (3)*, p. 115-128, pl. XV-XVI

ALLAN, R. S., 1937b, Two new Hutchinsonian (Tertiary) brachiopods from New Zealand. *Records of the Canterbury Museum 4 (3)*, p. 129-130, pl. XVII

ALLAN, R. S., 1937c, Tertiary Brachiopoda from the Mount Brown beds of Mount Donald, Weka Pass district, New Zealand. *Records of the Canterbury Museum 4 (3)*, p. 131-137, pl. XVIII

ALLAN, R. S., 1937d, Tertiary Brachiopoda from the Forest Hill Limestone (Hutchinsonian) of Southland, New Zealand. *Records of the Canterbury Museum 4 (3)*, p. 139-153, pl. XIX-XX

ALLAN, R. S., 1938a, Palaeontology, p. 60-63 *in* Speight, R., 1938, q.v.

ALLAN, R. S., 1938b, The Duntroonian Stage: a new division of the Oamaruian system, p. 89-92, Appendix *in* Speight, R., 1938, q.v.

ALLAN, R. S., 1940, Studies on the Recent and Tertiary Brachiopoda of Australia and New Zealand. Part II, *Records of the Canterbury Museum 4 (6)*, p. 277-297, pl. XXXV-XXXVII

ALLAN, R. S., 1949, Notes on a comparison of the Tertiary and Recent Brachiopoda of New Zealand and South America. *Transactions and Proceedings of the Royal Society of New Zealand 77 (5)*, p. 288-289

ALLAN, R. S., 1957, Appendix 3: Brachiopod faunas, p. 104-107 *in* Gage, M., 1957, q.v.

ALLAN, R. S., 1960, The succession of Tertiary brachiopod faunas in New Zealand. *Records of the Canterbury Museum 7 (3)*, p. 233-268

ALLAN, R. S., 1963, comments, p. 47 *in* Fleming, C. A., 1963, q.v.

FLEMING, C. A., 1963, Macrofossils, p. 33, 39-40, 46-49, 52-57, of Chapter 4 *in* Wilson, D. D., 1963, q.v.

GAGE, M., 1957, The Geology of Waitaki Subdivision. *Bulletin, New Zealand Geological Survey n.s. 55*, p. 1-135, 4 maps

SPEIGHT, R., 1938, The geology of the Mount Somers district. *New Zealand Department of Scientific and Industrial Research Geological Memoir 3*, p. 1-116, 1 map, 9 sections

WILSON, D. D., 1963, Geology of Waipara Subdivision. *Bulletin, New Zealand Geological Survey n.s. 64*, p. 1-122, 4 maps

2.3 Discussion

The empirical test of a species validity is that the species works. The above outline and discussion of the works of Thomson and of Allan demonstrates that their philosophies on speciation, and with the philosophies the species themselves, changed over time. Thomson stated (1926, p. 149) that brachiopod lists of Park and Uttley based on his conception of species up to that date required modification; so too do most present lists, according to Allan (1960). Foraminiferal dating further demonstrated the problems with previous classification schemes. Both Thomson and Allan readily admitted variability in species between localities, but neither seemed to as readily acknowledge variability *within* localities, preferring rather to apply what would now be viewed as a morphospecies or typological concept to the delineation of species. Thomson and Allan preferred to think in terms of polymorphs for the shape variants occurring in populous horizons such as the Rhizothyris-Pachymagas bed and the Mount Donald horizon. Thomson cited polymorphism in the specimens of the Rhizothyris-Pachymagas bed (Thomson 1920 p. 370), but still chose to differentiate species from the polymorphic assemblage; Allan (1960) later choosing to interpret the "polymorphic swarms" of the horizons as possible representatives of just a single species. As has already been suggested, both Thomson and Allan used the various brachiopod "series" in the sense of species, prompting Finlay & Marwick (1940, p. 116) to comment:

"The species of *Pachymagas* and *Rhizothyris* erected by Thomson are so very similar *inter se* and so variable in shape that the actual species present in these various greensands [of North Otago] appear to be much less important than the state of evolution of the genus as a whole..."

Much recent work on Cenozoic and Recent Brachiopoda has been aimed at defining population structures, the degree of intraspecific variation, and the possibilities of large-scale geographic variation (e.g. Aldridge 1981, 1990; Bowen & Campbell 1973; Chapman & Richardson 1981; Cohen et al. 1990; Dawson 1990b; Endo & Curry 1990; Lee 1978a, 1978b, 1980; Lee & Wilson 1979; Mineur & Richardson 1984; Richardson 1979, 1981a, 1981b, 1981c; Richardson & Mineur 1981; Schumann 1990; Stewart 1981). Such works as Wulff (1990) and Ghosh (1990) are also informative. In all cases, it is clear that a restudy along similar lines for all species that can be ascribed to *Waitakia* or *Waiparia* is warranted.

Chapter Three:

'SYSTEMATIC PALAEONTOLOGY'

Phylum **BRACHIOPODA** Dumeril, 1806

Class **ARTICULATA** Huxley, 1869

Order **TEREBRATULIDA** Waagen, 1883

Suborder **TEREBRATELLIDINA** Muir-Wood, 1955

Superfamily **TEREBRATELLOIDEA** King, 1850

Family **TEREBRATELLIDAE** King, 1850

Subfamily **TEREBRATELLINAE** King, 1850

Genus ***Waiparia*** Thomson, 1920

TYPE SPECIES: *Pachymagas abnormis* Thomson, 1917

STRATIGRAPHIC RANGE: Waitakian-Altonian (Early Miocene-Middle Miocene); New Zealand.

DIAGNOSIS: Small to Medium, smooth, weakly biconvex shells with ovate or suborbicular outlines; anterior commissure incipiently to moderately unisulcate. Beak sub-apicate, the well defined beak ridges meeting above the elongate non-circular to circular hypothyrid foramen. Cardinal area gently convex, with disjunct or conjunct deltidial plates. Shell interior demonstrating some secondary shell thickening of the posterior; cardinal process small, with wing-like projections of myophore that develop posteriorly and showing development of an anterior swelling that projects ventrally. Median septum slender to relatively thickened, extending anteriorly about one-third of

valve length, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped shallowly excavate hinge-trough with steeply inclined walls; crural bases fused to the thickened inner socket ridges. Adult loop trabecular.

DISCUSSION: Beak characteristics of this genus serve to distinguish it from the related genus *Waitakia*. While the characteristics of the beak seem to suggest strong pedicle attachment, lithologies in which the genus is commonly found suggest a free-lying habit. The origins of the genus are not clear, but it is considered that the genus evolved directly from *Waitakia elliptica* or from a pre-Duntroonian common ancestor. The genus has only been recognised in publication from New Zealand, but probably occurs in Antarctica (section 1.2)

3.0 ***Waiparia abnormis*** (Thomson, 1917)

SYNONYMY:
Pachymagas abnormis Thomson, 1917, p. 403, 412
Pachymagas abnormis Thomson, 1918b, p. 197
Waiparia abnormis Thomson, 1920, p. 381, Pl. XXVI, figs. 16-18
Waiparia abnormis Allan, 1937c, p. 136
Waiparia abnormis Allan, 1957, p. 107
Waiparia abnormis Allan, 1960, p. 243, 246
Waiparia abnormis Hatai *in* Muir-Wood et al. 1965, p. H855
Waiparia abnormis Keyes, 1971, p. 83
Waiparia abnormis Dawson, 1990a, p. 76

TYPE LOCALITY: "Sands interbedded with the main Mount Brown limestone, cuesta overlooking the Weka Pass, Canterbury" (Allan 1937c). The "Mount Donald horizon" (Allan 1937c and see fig. 11) at the base of the upper 'lens' (Browne & Field 1985) of the Main Mt Brown Limestone Member of the Mt Brown Formation, Weka Pass, North Canterbury.

TYPE MATERIAL: Holotype and paratypes (Br 113), 23 paratypes (B903), and 25 unnumbered paratypes in the National Museum of New Zealand, Wellington.

(Source: Dawson 1990a)

OCCURRENCE: Main Mt Brown Limestone (base of) {North Canterbury}, at: Weka Pass; Gee Greensand {North Otago}, at: All Day Bay; Concord Greensand {Otago}, at: Seacliff; Caversham Sandstone {Otago}, at: Waikouaiti (?); Tarakohe mudstone {Nelson}, at: Aorere and Brown River junction, Takaka (?); Calamity Point Sandstone {Southland}, at: Clifden; Ihungia beds {Gisborne}, at: Whatatutu.

MATERIAL EXAMINED: Material from the Allan Collection, University of Canterbury: (970, 971, 973, 974, 976-979, 983-985 Weka Pass) ; (26169, 26174, 26176, 26177 Clifden) ; (26651, 26653 Seacliff) ; (26736, 26737 All Day Bay) ; (28442 Weka Pass) ; (28561, 28563-28570 Weka Pass) ; (26169, 26174, 26176, 26177 Clifden). Material from Department of Geology, University of Otago: (5275 Clifden). Unnumbered collections, University of Canterbury, Department of Geological Sciences: (Weka Pass (bag): S. Fryer MSc. Thesis Collection) ; (Weka Pass (bag): D. I. MacKinnon Collection).

AGE/RANGE: Waitakian – Altonian

FIGURES: 12-14

DESCRIPTION: Small, smooth, shallowly biconvex shell displaying numerous faint growth lines; shell usually ovate though some specimens are suborbicular or, rarely,

sub-quadrate; relatively wide cardinal margin gently curved, almost straight; anterior commissure rectimarginate to incipiently unisulcate. Beak high, obtuse; large, elongate non-circular hypothyrid foramen; beak ridges well defined and sharp, meeting above the foramen; gently convex cardinal area with disjunct deltidial plates or deltidial plates that are conjunct only at their bases; prominent ventral palintrope high and wide. Median septum slender, extending anteriorly about one-third of valve length, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped shallowly excavate hinge-trough with steeply inclined walls; crural bases fused to the thickened inner socket ridges. Cardinal process consisting of roughened myophore with a boss-like anterior swelling which occupies the posterior one-quarter to one-third of the hinge-trough; incipient wing-like projections of myophore develop posteriorly. Dorsal adductor muscle scars relatively large and distinct, terminating anteriorly at approximately the termination point of the median septum – at one-third the length of the valve. The relatively large muscle-field scars of the ventral valve are impressed such as to produce a low median ridge in the valve floor between the scars. The teeth are large and sturdy, and are perched on swollen bases, which are shallowly grooved to accommodate the swollen inner socket ridges. Adult loop trabecular, the transverse connecting band rather attenuated.

DISCUSSION: Thomson's basis for the establishment of the genus *Waiparia*, with *Pachymagas abnormis* as its genotype, rests largely on characteristics of the beak. The beak of *abnormis* does significantly differ from the majority of New Zealand specimens ascribed to *Pachymagas* in that the foramen is hypothyrid, and the beak is not truncated. Buckman *in litt.* (Thomson 1918b, p. 197) suggested that a new genus

should be established in light of the species distinct beak characters, Thomson (1920) later obliging.

The original description for *P. abnormis* neglected mention of interior characteristics other than noting the possession of a small cardinal process; however in his generic description, Thomson (1920, p. 380) states: "Cardinalia similar to those of young specimens and primitive species of *Pachymagas*, with strong socket-ridges but a slender septum, a hinge-trough with flatly inclined walls and a small cardinal process confined to the umbo." While Thomson stated that the walls of the hinge-trough of *Waiparia* are flatly inclined, it was found that the walls are relatively steeply inclined in adults of both *Waiparia abnormis* and *intermedia*. Further, the cardinal process of *W. abnormis* from Weka Pass, while admittedly being confined to the umbo, doesn't in fact closely resemble the process of young specimens of *Pachymagas*; rather it develops the anterior boss-like swelling and posterior wing-like projections of myophore common to adult specimens, although admittedly being small (see fig. 14a, b). A single interior observed from Waitakian Concord Greensand at Seacliff demonstrated a very small cardinal process confined to the posterior of the hinge-trough, possessing no boss-like anterior swelling as in the specimens from Weka Pass. However, the walls of the hinge-trough were still observed to be relatively steep, not shallow as Thomson's (1920) diagnosis suggests. Interiors of adult *W. abnormis* from Weka Pass are compared with interiors of juvenile *W. cottoni* from the Mount Donald horizon at Weka Pass in figure 14.

It is important to note that the holotype of *W. abnormis* (see figure 12 and Thomson 1920, pl. XXVI, figs. 16-18) is not really representative of the species typical form, the shell being rounded in outline rather than ovate. It could readily be

postulated, on examination of the respective holotypes of *W. abnormis* and *W. intermedia*, and with regard to Thomson's assertion that large specimens of *W. abnormis* are found in the "Rhizothyris-Pachymagas bed" (Fleming 1963), plus consideration of both species reputed occurrence in the Rifle Butts mudstone at All Day Bay (Thomson 1918b; 1920), that *abnormis* and *intermedia* are synonyms for the same species. The reputed co-occurrence of *abnormis* and *intermedia* by Thomson extends to strata other than the Rifle Butts mudstone and "Rhizothyris-Pachymagas bed". Thomson (1917; 1918b; 1920) additionally reported both *abnormis* and *intermedia* from the Caversham Sandstone (Central Otago) and the Tarakohe mudstone (Takaka). Allan (1937c) broadened this co-occurrence when he recorded a "single typical specimen [of *W. intermedia*]" from the Mount Donald horizon of Weka Pass.

It is considered likely that the large specimens of '*W. abnormis*' recorded from the *Pachymagas* bed are in fact typical specimens of *W. intermedia* rather than large specimens of *W. abnormis* with the atypical shape of the holotype. *Waiparia abnormis* does not appear to occur in the "Rhizothyris-Pachymagas bed". Thomson's (1918b) record of *W. abnormis* from the Caversham Sandstone at Waikouaiti is doubtful, and probably represents recognition of juveniles of *W. intermedia*. *Waiparia abnormis* certainly occurs in the Concord Greensand at the base of the Caversham Sandstone, and probably the basal Caversham Sandstone of Otaian age (Toha 1993). The species present in the upper Caversham Sandstone, of Altonian age (Toha 1993), is *W. intermedia*, again juveniles confusing matters by their resemblance to *W. abnormis*. The species present in the Rifle Butts mudstone at All Day Bay is likewise *W. intermedia*. Though *abnormis* was not recognised from Rifle Butts mudstone

during this study, it was found in the basal (Waitakia) Gee Greensand at All Day Bay. The record (Thomson 1917) of *W. abnormis* from Tarakohe cannot be confirmed or refuted, as no material from there was examined, the exposure at Tarakohe Quarry not accessible during a visit due to blasting. The species occurs at Clifden, the records of the Allan Collection giving no information as to the stratigraphic position it was collected from, but a single specimen (5275) found in the collections at the University of Otago comes from the Calamity Point Sandstone at Clifden; the specimens in the Allan Collection could have been collected from this same lithology.

As is implied above, *W. abnormis* and juveniles of *W. intermedia* are difficult to differentiate, one from the other. The two can be differentiated as, usually, juveniles of *W. intermedia* are suborbicular where specimens of *abnormis* are ovate; the foramen of *abnormis* is also characteristically elongate non-circular, while that of *intermedia* is often circular. Small juvenile forms of *intermedia* are indistinguishable from juveniles of *abnormis*, both being ovate in outline. Examination of the growth-lines on the shells of *W. intermedia* suggests that the species could be considered just a large *W. abnormis*, though growth trajectories of *intermedia* change with size, the hinge-line becoming progressively wider and the shell more rounded overall. *Waiparia abnormis* and *W. intermedia* should be retained as separate species as the earliest representatives are all of small size, with no real suggestion that the size is dependent on environment, nor that *W. abnormis* is merely the juvenile stage of *W. intermedia*, as growth-line crowding in *abnormis* suggests that specimens are adults.

Biernat et al. (1985) compared the observed beak characteristics of their *Pachymagas* cf. *cottoni* (a species strongly resembling *W. abnormis*, and probably congeneric – see sect 1.2) with those of figure 2E (*Magellania flavescens*) of

Richardson (1981a), implying possession of an inert (Richardson 1979) pedicle. While the size of the foramen is not directly indicative of the size or strength of the pedicle itself (Richardson 1981a), beak shape of *abnormis* might rather suggest a comparison with figure 2C (*Terebratella inconspicua*) of Richardson (1981a), suggestive of possession of a transitional (Richardson 1979) pedicle. The pedicle could not have been muscular (Richardson 1979), as dorsal pedicle adjustor muscle scars are present on the hinge-plates. These points considered, *Waiparia abnormis* probably attached closely (and firmly?) to whatever substrate it was originally attached, the beak showing no evidence of attrition, therefore rotation of the shell was presumably minimal. The species is usually (apart from evidently very sparse occurrence in the Gee and Concord Greensands) found associated with fine sandstones and mudstones of mid-outer to middle shelf depths (Mt Brown Formation (Browne & Field 1985); Caversham Sandstone (Toha 1993)), suggesting that the species lived on such sediment, presumably in a free-lying habit (Richardson 1981c). The shell may have found attachment on shelly debris or other, suitably substantial, surfaces in such a substrate.

It is conceivable that the species is actually a shallow water form, the strong attachment and shallow convexity of the form adaptations to turbulent waters. However, such a shallow water form would require transportation offshore to environments where the substrates in which it is found originally accumulated; the conjoined nature of the majority of the valves seem to preclude this. *Waiparia abnormis* must therefore be considered a moderately deep water form.

Thomson stated that the genus *Waiparia* "may be considered as springing from the same stock as *Pachymagas*, but lagging behind in foraminal evolution. It

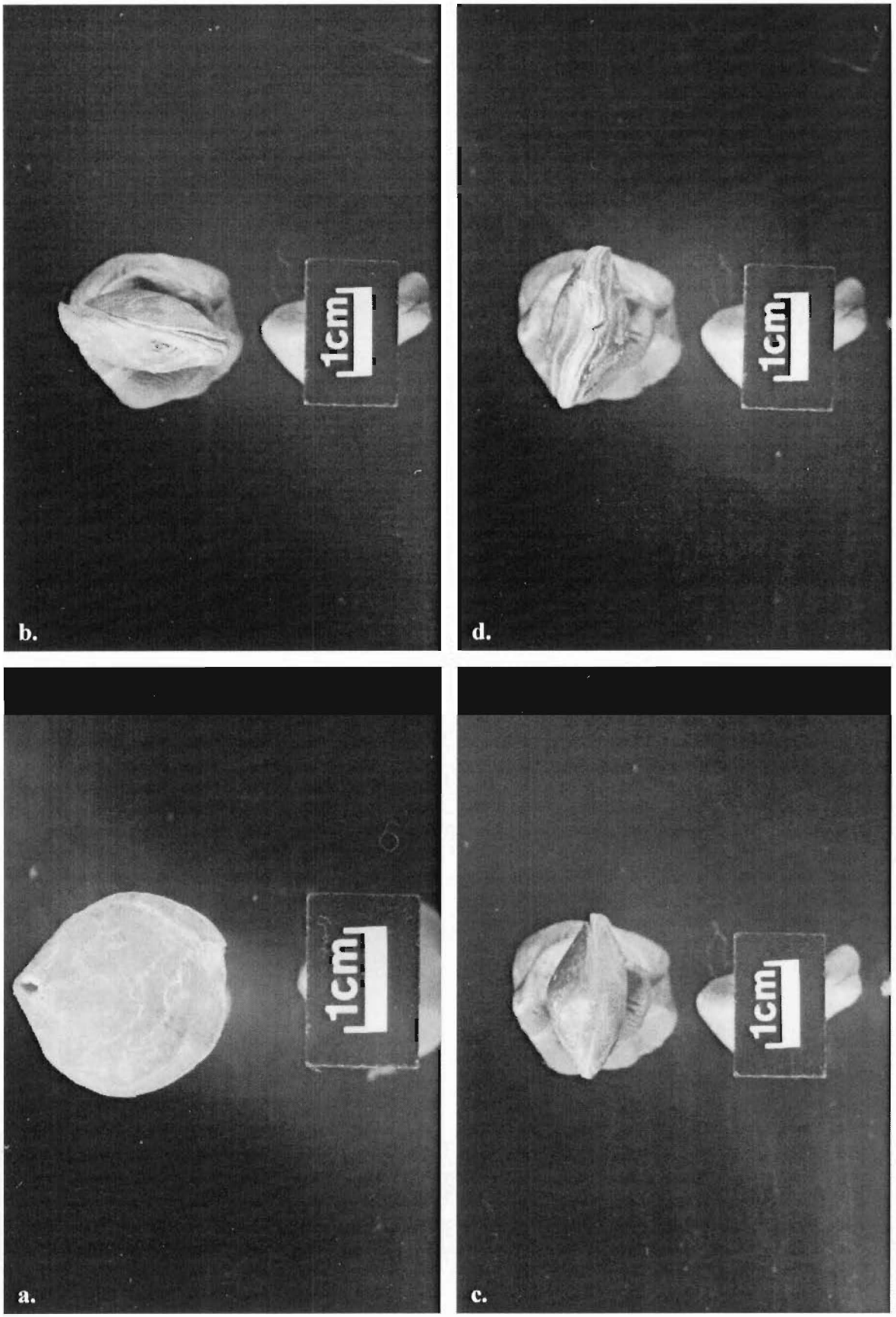


Figure 12. Holotype of *Waiparia abnormis* (Br 113).

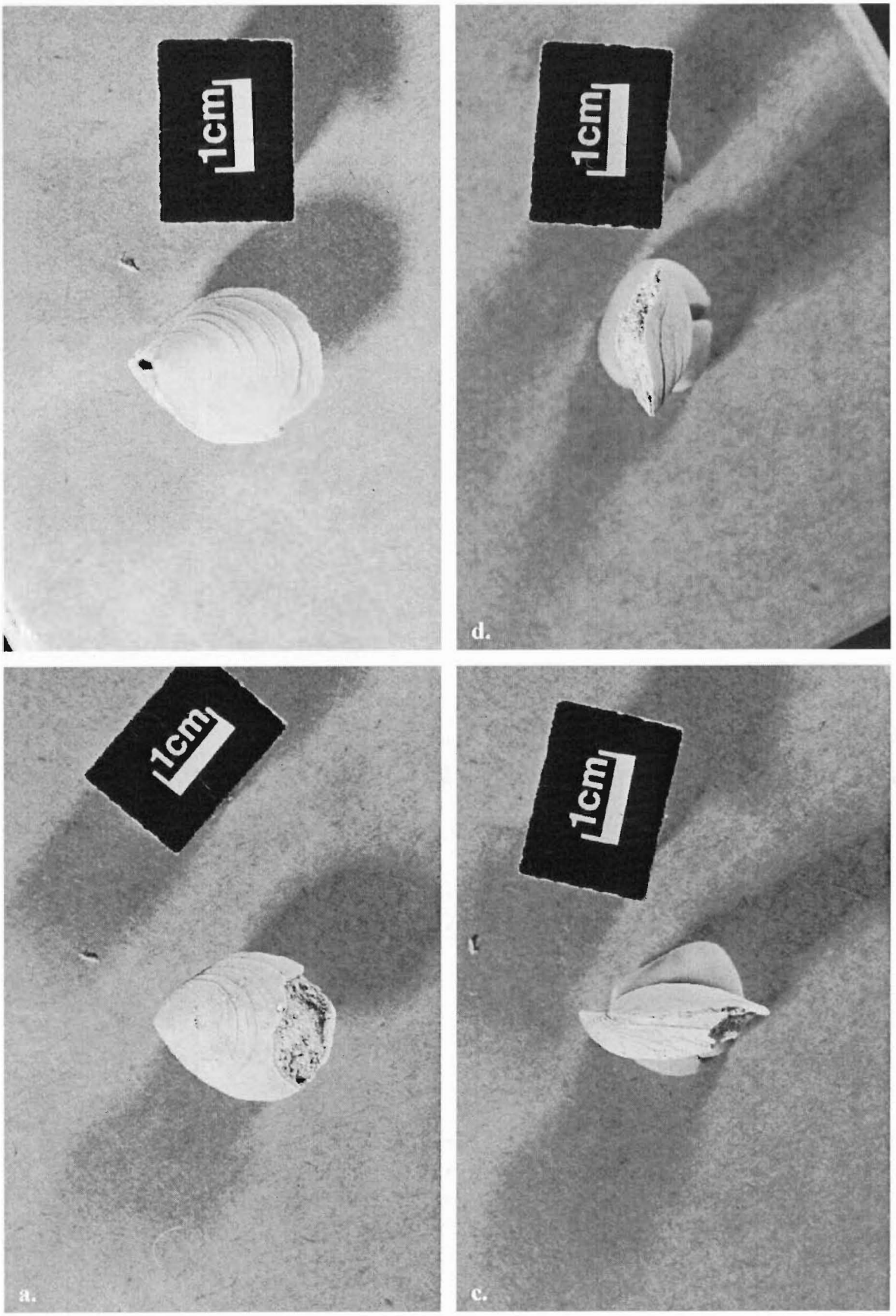


Figure 13. *Waiparia abnormis* (Allan Colln. 968) from Weka Pass.

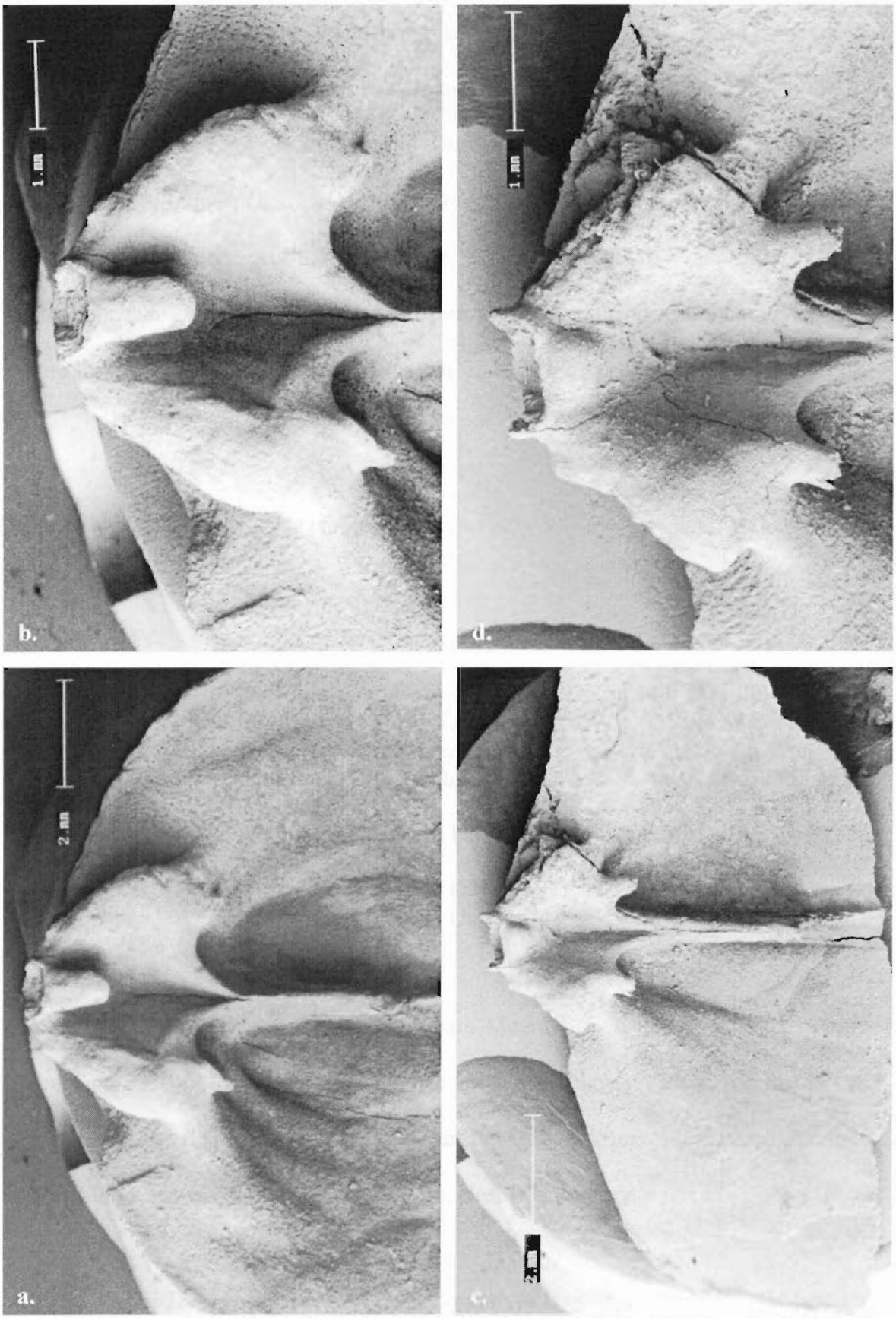


Figure 14. Comparison of adult *Waiparia abnormis* dorsal interiors (**a**, **b**: UCM 2006) with juvenile *Waitakia cottoni* dorsal interiors (**c**, **d**: UCM 2007). Both specimens from Weka Pass.

possibly gave rise directly to *Pachymagas* of the type *P. ellipticus*, which possesses a foramen which is submesothyrid, but almost mesothyrid" (Thomson, 1920, p. 380). Thomson must have been implying a Duntroonian or earlier common ancestor, because *P. ellipticus* (*Waitakia elliptica*) appears to occur in earlier geological horizons than does either of the two species Thomson referred to *Waiparia* in 1920. It is thought that examination of material from the Wharekuri Greensands might shed some light on the origins and development of both *Waiparia* and *Waitakia* (section 4.0).

3.1 *Waiparia intermedia* Thomson, 1920

SYNONYMY:

Waiparia intermedia Thomson, 1920, p. 381, pl. XXVI, figs. 13-15
Waiparia intermedia Thomson 1926, p. 149, 151, 156
Waiparia intermedia Thomson, 1927, p. 285, text fig. 97a-c
Waiparia intermedia Allan, 1957, p. 107
Waiparia intermedia Allan, 1960, p. 243, 245, 268 (stratigraphic range)
Waiparia intermedia Hatai *in* Muir-Wood et al. 1965, p. H855, text fig. 739, 2a-c
Waiparia intermedia Keyes, 1971, p. 83
Waiparia intermedia Dawson, 1990a, p. 77-78

TYPE LOCALITY: "Foot of dip-slope, main Mount Brown limestone, Weka Pass" (Thomson 1920). "Rhizothyris-Pachymagas bed" (Fleming 1963 and see fig. 11) at top of upper 'lens' (Browne & Field 1985) of the Main Mt Brown Limestone Member of the Mount Brown Formation, Weka Pass, North Canterbury.

TYPE MATERIAL: Holotype (Br 117) and paratype (B 909) in the National Museum of New Zealand, Wellington.

(Source: Dawson 1990a)

OCCURRENCE: Main Mt Brown Limestone {North Canterbury}, at: Weka Pass; Rifle Butts Formation {North Otago}, at: All Day Bay; Tarakohe mudstone {Nelson}, at: Aorere and Brown River junction, Takaka (?); Caversham Sandstone {Otago}, at: Caversham, Karitane, Seacliff, Waikouaiti, Puketeraki.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (1488-1492 All Day Bay) ; (26638-26650 Waikouaiti) ; (26654-26669, 26671-26678 Seacliff) ; (26679-26680 Caversham) ; (26686, 26688, 26689, 26691 Karitane) ; (26692-26697 Karitane) ; (26787-26789, 26790, 26791, 26794-26801 All Day Bay). Material from Department of Geology, University of Otago: (ZD 10, 9 specimens, Main Mt Brown Limestone).

AGE/RANGE: Altonian

FIGURES: 15-17

DESCRIPTION: Relatively small to medium, smooth, biconvex shell displaying numerous faint growth-lines; shell suborbicular; wide cardinal margin gently curved, almost straight; anterior commissure weakly broadly unisulcate. Beak high, obtuse; medium to large elongate non-circular to circular hypothyrid foramen; beak ridges well defined and sharp, meeting above the foramen; gently convex cardinal area with disjunct or conjunct deltidial plates; prominent ventral palintrope high and wide. Median septum slender to relatively thickened, extending anteriorly about one-third of valve length, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped

hinge-trough with steeply inclined walls; crural bases fused to the thickened inner socket ridges. Cardinal process consisting of roughened myophore with a boss-like anterior swelling which occupies the posterior one-quarter to one-third of the hinge-trough; incipient wing-like projections of myophore develop anteriorly. Dorsal adductor muscle scars relatively large and distinct, terminating anteriorly at approximately the termination point of the median septum – at one-third the length of the valve. The teeth are large and sturdy, and are perched on swollen bases, which are grooved to accommodate the swollen inner socket ridges. Adult loop trabecular.

DISCUSSION: As Thomson (1920) indicates, specimens of *W. intermedia* that are found in the limestone at Weka Pass are quite strongly convex, more so than those specimens that occur in other lithologies, the difference in convexity perhaps indicating a difference in the size of the lophophore. McCulloch (1981) interprets the limestone lenses of the Mt Brown Formation as redeposited accumulations of an originally shallow shelf, sandy shore fauna.

As has been suggested in discussion of *W. abnormis* (q.v.), the shallowly convex nature of *W. abnormis* indicates a small lophophore that might have operated best under energetic conditions – e.g. turbulent near-shore waters, though its occurrence in deep water deposits appears to rule this interpretation out. The fact that *W. intermedia* is atypically strongly convex, by inference possessing a large lophophore, where it is more shallowly convex in the Caversham Sandstone and Rifle Butts mudstone could indicate that in the instance of its occurrence in the Main Mt Brown Limestone, it occupied a deeper water environment than the more shallowly convex representatives of the species. Its occurrence in the lower member of the Caversham Sandstone, interpreted by Toha (1993) to have accumulated from outer

shelf to mid-outer shelf depths (shallowing upward from Otaian to Altonian times), does not lend support to a correlation between shallow water depth (high hydrodynamic regime) and low convexity of the shell, as the specimens found are not as convex as the shallower? water Main Mt Brown Limestone specimens. Its further occurrence in the Rifle Butts mudstone, a deep water deposit (e.g. Lee et al. 1996), suggests that the species was probably free-lying (c.f. *Waiparia abnormis*, section 3.0). The species is found in the middle member of the Caversham Sandstone also, the deposition of which has been interpreted by Toha (1993) to have occurred in inner shelf depths. The species therefore probably lived as a free-lying form on substrates of the middle to inner shelf. A reconstruction of original population structure would no doubt help greatly in interpretations of original lifestyle (Stewart 1981).

The record (Thomson 1920) of *W. intermedia* from the mudstone at the junction of the Aorere and Brown Rivers cannot be confirmed or refuted, as no material from there was examined, the exposure at Tarakohe Quarry not accessible during a visit due to blasting. Thomson's (1920; 1926) record of *W. intermedia* from the Wharekuri Greensand is very interesting because the greensand is of Whaingaroan age (e.g. Fordyce 1996). This record places *intermedia* in strata older than that in which *Waitakia elliptica* is found, and understandably has far-reaching implications for the origins and evolution of both *Waiparia* and *Waitakia*. While discussion of these possible implications is made in section 4.0, it should be noted here that Thomson's record of *W. intermedia* represents rather *Waiparia abnormis*, *Waitakia elliptica*, or perhaps a common ancestor of both genera. Thomson himself stated that the single specimen he had examined was "difficult to distinguish from *Waiparia intermedia*, but perhaps a member of the *Pachymagas ellipticus* [*Waitakia elliptica*]

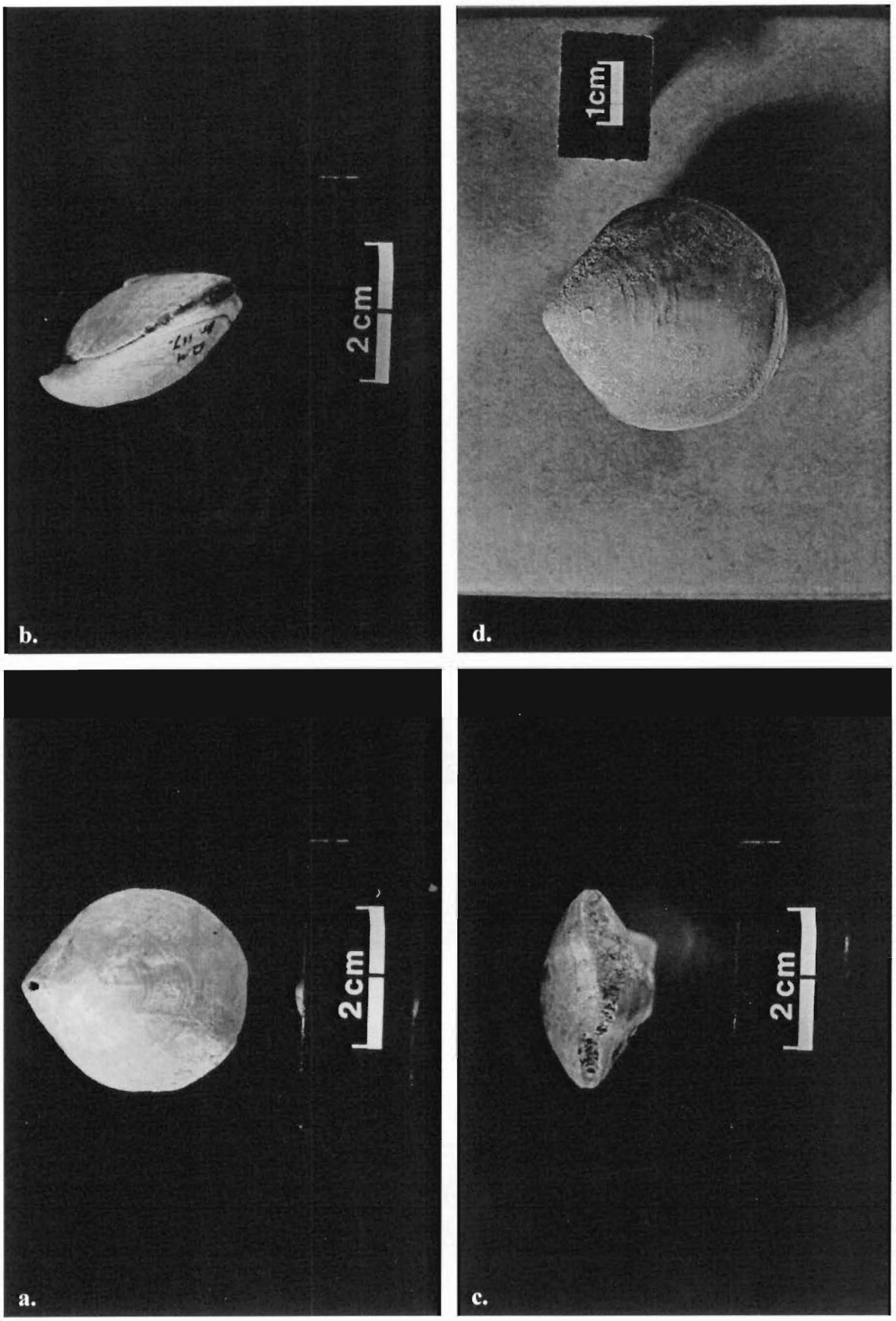


Figure 15. Holotype (**a**, **b**, **c**: Br 117) and ventral exterior (**d**: Allan Colln. 26687; Karitane) of *Waiparia intermedia*.

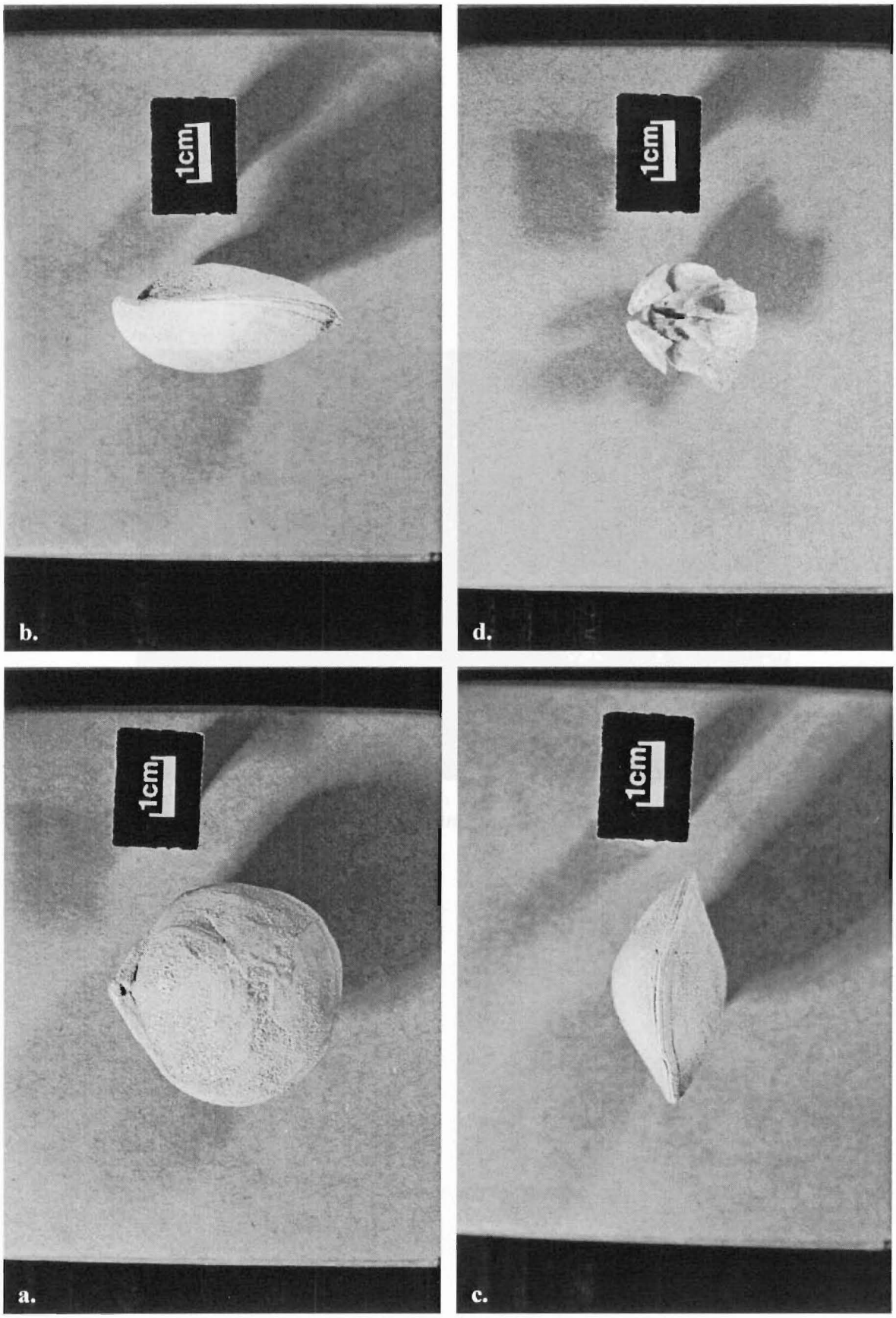


Figure 16. Exteriors (**a**, **b**, **c**: Allan Colln. 26687) and dorsal interior (**d**: Allan Colln. 26697) of *Waiparia intermedia* from Karitane.

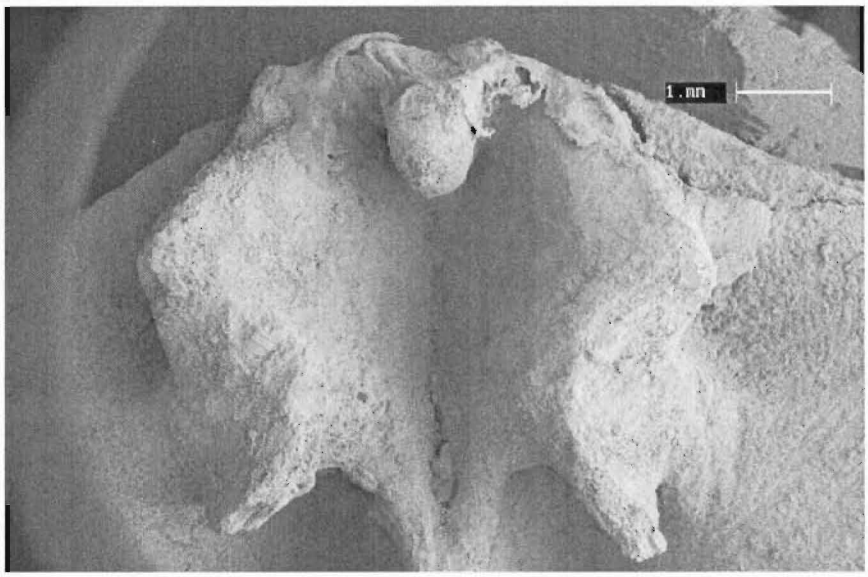


Figure 17. Dorsal interior of *Waiparia intermedia* (ZD 10) from Weka Pass.

series" (Thomson 1926, p. 156). A small number of specimens from the Wharekuri Greensand (Otago University, collection no. 6569) were examined, but it could not be determined on the evidence of these few fragmentary specimens whether the species present is *Waiparia abnormis* or *Waitakia elliptica*, or the ancestral form of both, the specimens appearing to possess characteristics of both genera. The significance of the Wharekuri Greensand material was only recognised late in the study, consequently additional material has not been collected from the locality, and has to be a goal of future study of the genera.

3.2 *Waiparia* horizons at All Day Bay, Oamaru

A stratigraphic column for Campbell's Beach – All Day Bay – Kakanui is shown in figure 18 Of significant note is the fact that the lowermost exposure of Gee Greensand in the area is Waitakian in age (Allan 1957 – the basal 1.5 metres of greensand is Waitakian on foraminiferal evidence). Specimens 26736 and 26737 of the Allan Collection (Canterbury University), which are here referred to *Waiparia abnormis*, are recorded as coming from the lower few feet of the greensands at All Day Bay. This record places these specimens in the Waitakian. Although All Day Bay has been visited on three separate occasions, additional specimens were not located, despite a specific search for *abnormis* during the last visit. There is no reason to doubt that the Allan Collection specimens come from this locality, and so the assumption must be made that *abnormis* is very rare there. This record, along with two specimens identified from the Concord Greensand at Seacliff, extends the range of *abnormis* into the Waitakian.

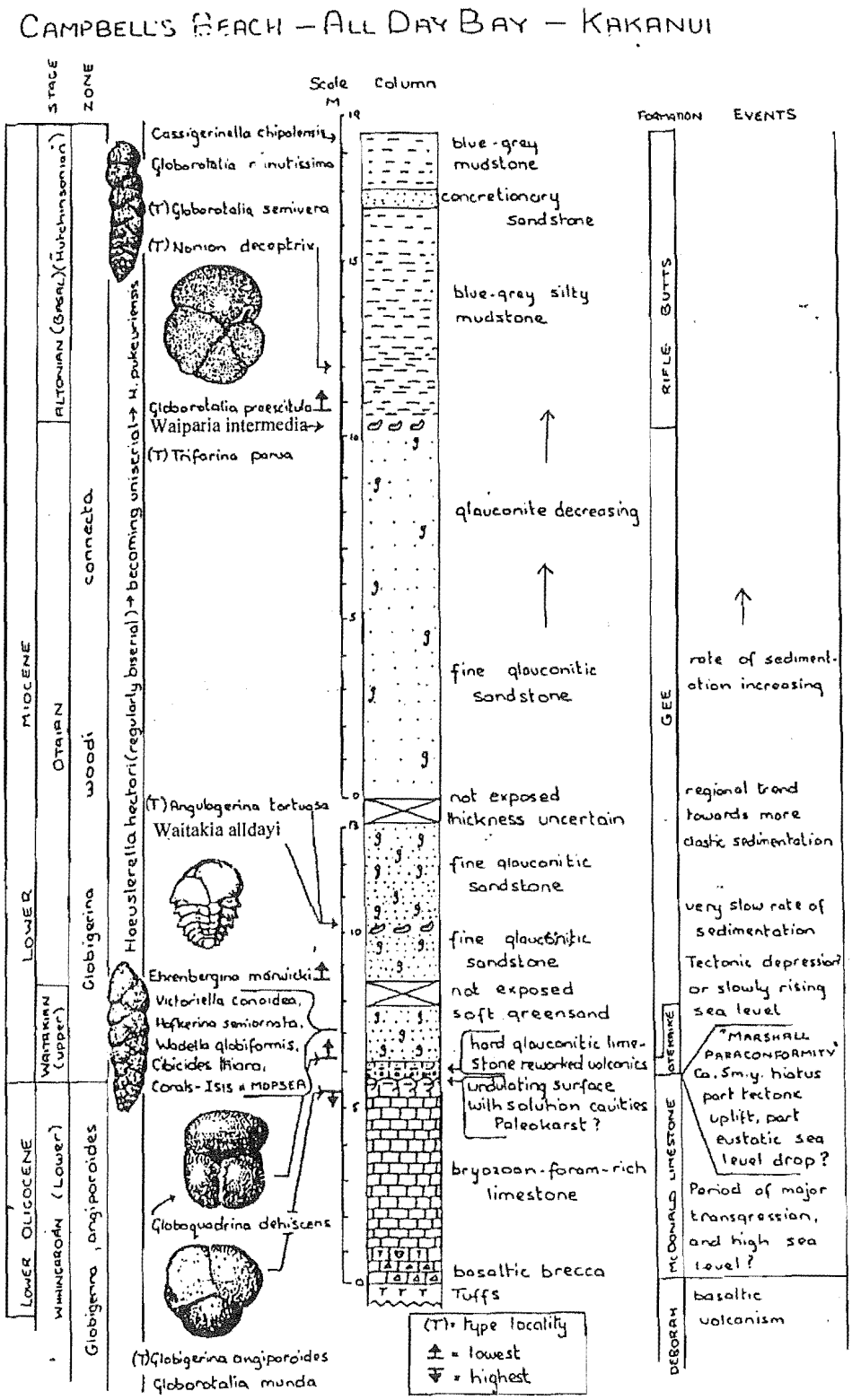


Figure 18. Stratigraphic column for Campbell's Beach – All Day Bay – Kakanui demonstrating lower *Waitakia alldayi* horizon and upper *Waiparia intermedia* horizon. Note the Waitakian age of the basal Gee Greensand. (Modified from Hornibrook 1982)

Waiparia abnormis does not appear to accompany the brachiopods described from the basal "Isis bed" itself (fig. 18), viz. *Aetheia gualteri* (Morris), *Tegulorhynchia squamosa* (Hutton), *Campages neozelanica* Allan, and "*Terebratella*" n. sp. (e.g. Lee 1990; Fordyce, Hornibrook & Maxwell 1985). The storm concentrated? (Lewis & Belliss 1984) octocorals are now referred to *Keratoisis* and *Primnoisis* rather than *Isis* and *Mopsea*, respectively (Lee 1990). The basal greensands at nearby Gee's Point were also examined for *W. abnormis*, but while there appeared to be a greater incidence of fossil brachiopods compared to the basal greensands at All Day Bay, no specimens of *abnormis* were located here either.

Thomson (1918b) recorded a single specimen of *abnormis* from the "Hutchinsonian" greensands of All Day Bay, though an exact stratigraphic position was not given. Thomson (1918b, p. 197) also mentions the occurrence of *W. abnormis* in the "Awamoan" mudstones of All Day Bay. Later Thomson (1920) recorded flattened specimens of *W. intermedia* as coming from the same mudstones. Thomson (1926, p. 149) stated that "...at All Day Bay there is a higher division present [within the "Hutchinsonian" greensands] containing only the species *Waiparia intermedia* Thomson." He further describes this *W. intermedia* fauna as occurring "...through a considerable thickness of beds probably upwards of 50 ft., which gradually lose their rich content of glauconite and become more argillaceous" (Thomson 1926, p. 151).

Allan (1957) recognised a "lower *Waiparia* bed" and an "upper *Waiparia* bed" at All Day Bay, and remarked that the lower and upper *Waiparia* beds at All Day Bay are shown, respectively, to be of Otaian and "Hutchinsonian" ages on foraminiferal evidence. Allan was uncertain from which horizons Thomson had collected *abnormis* and *intermedia*, and commented that:

"Thomson was unaware that there were two *Waiparia* horizons at All Day Bay; likewise the writer's collections at this locality were made before this discovery. Consequently new collections are necessary to determine whether there are significant differences between the *Waiparias* of the Otaian and the Hutchinsonian horizons..." (Allan 1960, p. 243)

Allan (1960) stated that no brachiopods had been described from the lower *Waiparia* beds at All Day Bay. This horizon has been recollected, and it can be stated that the brachiopod present in abundance is *Waitakia alldayi* n. sp.; there do not appear to be any specimens referable to either *W. abnormis* or *W. intermedia* from this horizon.

Allan's uncertainty over which horizons Thomson collected *abnormis* and *intermedia* from is slightly puzzling, as Thomson clearly records the collection of both *abnormis* and *intermedia* from the mudstones/blue clays (Rifle Butts Formation) – Allan's upper *Waiparia* bed, and recorded *intermedia* as extending at least 15 m. (50 ft.) downward through the greensands from the argillaceous beds. It seems likely that Thomson did collect from the lower brachiopod horizon too, but placed the specimens in the genus *Pachymagas*, recording *P. haasti*, *P. hectori*, and *P. marshalli* from All Day Bay (Thomson 1920, 1926).

As stated, Thomson recorded both *W. abnormis* and *intermedia* from the upper horizon at All Day Bay. However, it is contended (see section 3.0) that Thomson misidentified juveniles of *W. intermedia* as adult *W. abnormis* at All Day Bay, and at other localities. It is considered that *abnormis* is absent from the Allan's upper *Waiparia* horizon at All Day Bay.

Allan's assertion that Thomson did not know that there were two *Waiparia* horizons at All Day Bay may be invalid because it is probable that Thomson did not consider the lower horizon a *Waiparia* horizon at all, but rather a *Pachymagas* horizon. Collections from the lower brachiopod horizon at All Day Bay yield *Waitakia alldayi* of this study (section 3.3).

To summarise, *W. abnormis* was collected by Allan from within the lowest 1.5 metres of the greensands at All Day Bay, and is Waitakian in age. The lower brachiopod bed (fig. 18) contains *Waitakia alldayi* n. sp. The author has noted the sporadic occurrence of *W. alldayi* upward through the greensands a distance of approximately 4-5 metres above this bed (where exposure is lost). From examination of specimens in the collections at Canterbury and Otago Universities, it is evident that the only occurrence of brachiopods at All Day Bay referable to *W. intermedia* occur in the mudstones of the Rifle Butts Formation. Thomson's record of *W. intermedia* extending through at least 15 m. of the greensands is based on misidentification of *Waitakia alldayi* n. sp.

Genus ***Waitakia*** gen. nov.

ETYMOLOGY: Named from Waitaki Valley where species of the genus occur in great abundance.

TYPE SPECIES: *Pachymagas ellipticus* Thomson, 1918

STRATIGRAPHIC RANGE: Duntroonian-Clifdenian? (Late Oligocene-Middle Miocene); New Zealand.

DIAGNOSIS: Medium to large, smooth, biconvex shells typically with ovate or elliptical outlines; anterior commissure weakly sulcate to very strongly unisulcate. Beak erect to suberect, attrite, foramen small, submesothyrid to mesothyrid. Beak ridges well defined, sometimes bounding prominent ventral palintrope; cardinal area gently convex, with conjunct deltidial plates or symphytium. Shell interior demonstrating extensive secondary shell thickening of the posterior; secondary thickening of cardinal elements restrict hinge-trough; cardinal process small to large, with wing-like projections of myophore that develop posteriorly and showing development of an anterior swelling that projects ventrally. Median septum thickened, extending anteriorly about one-third the length of the valve, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped hinge-trough with steeply inclined walls; crural bases fused to the thickened inner socket ridges. Adult loop trabecular.

DISCUSSION: Beak characteristics of this genus serve to distinguish it from the related genus *Waiparia* Thomson. The suberect to erect beak, along with its attrite nature suggest that the pedicle was active, though secondary shell thickening suggests that the shell was probably free-lying on soft substrates. The shell was perhaps tethered to bioclastic fragments within the substrate, the pedicle probably enabling slight repositioning of the adult shell, the genus effectively free-lying. Stewart (1981) found that histograms made for benthic death assemblages of present day free-lying *Terebratella inconspicua*, *Terebratella sanguinea*, and *Neothyris lenticularis* were all unimodal and right-skewed with an absence of juveniles. Most of the histograms constructed for the species of *Waitakia* in this chapter are similar, lending further weight to the suggestion that these species were free-lying. The youngest members of

the genus begin to demonstrate a loss of the transverse connecting band, total loss of which marks the transition to the genus *Neothyris*.

3.3 *Waitakia alldayi* n. sp.

SYNONYMY:
Magellania sinuata Thomson, 1908, p. 101, pl. XIV, fig. 3 (not of Hutton 1873)
Pachymagas parki Thomson, 1918b, p. 197
Pachymagas marshalli Thomson 1920 (in part), p. 375
Pachymagas marshalli Thomson, 1926, p. 150
Pachymagas cottoni Thomson, 1927, fig. 29a

ETYMOLOGY: Named from All Day Bay, the type locality for the species.

TYPE LOCALITY: Gee Greensand, All Day Bay, North Otago

TYPE MATERIAL: Holotype (Allan Colln. 26735) and paratypes (Allan Colln. 26720-26734, 26739-26783; UCM 2008) in the Department of Geological Sciences, University of Canterbury, Christchurch.

OCCURRENCE: Gee Greensand {North Otago}, at: All Day Bay, Gee's Point, Campbell's Beach, Kakanui.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (1498-1504 All Day Bay) ; (26720-26783 All Day Bay) ; (27374-27394 Kakanui) ; (27396-27401 Kakanui) ; (27408, 27410-27413, 27417, 27419-27420, 27422-27423 Kakanui). Unnumbered collections, University of Canterbury: (All Day Bay (3 bags), Gee's Point (bag): S. Fryer MSc. Thesis Collection).

AGE/RANGE: Waitakian – Otaian

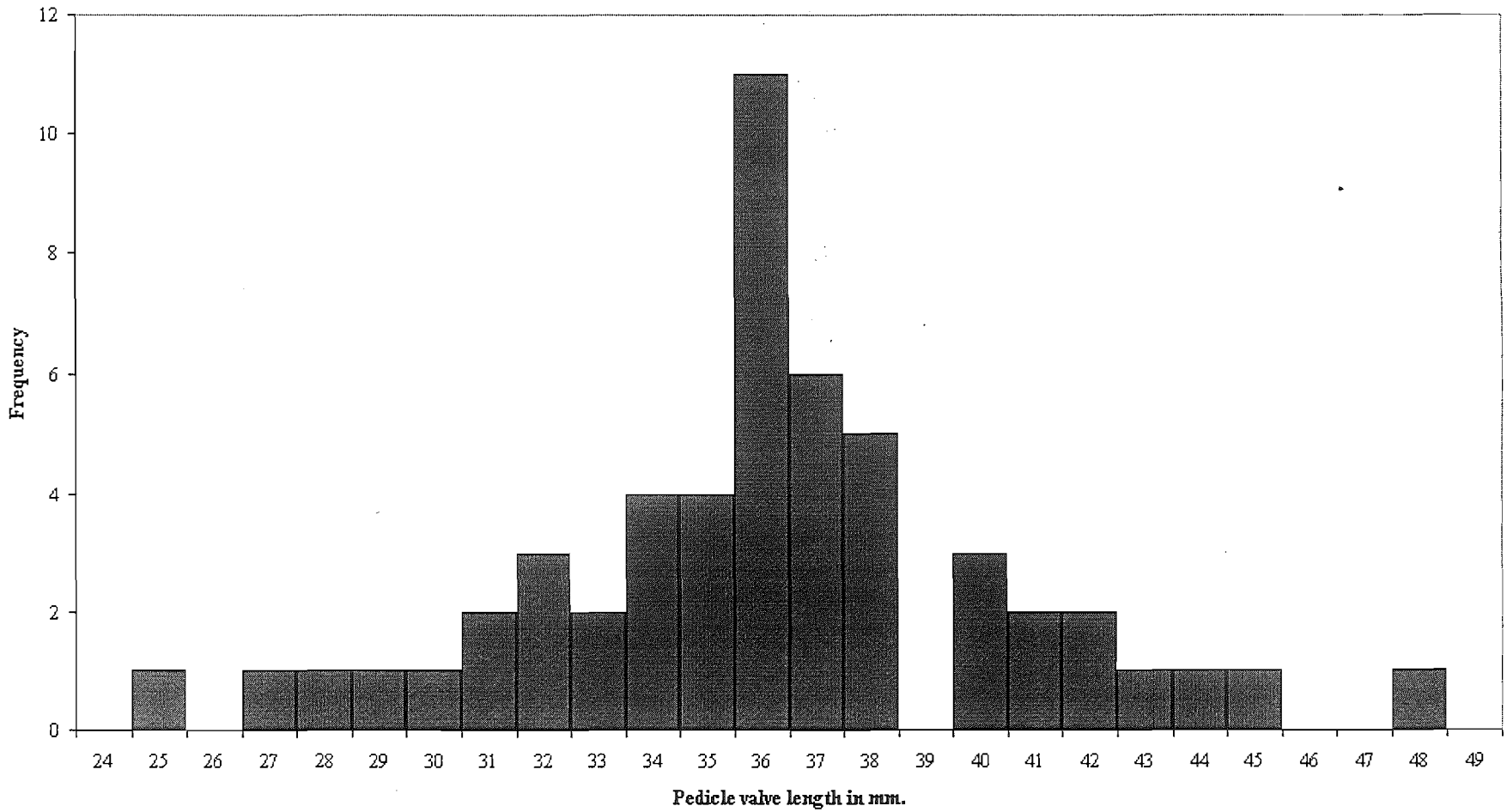
FIGURES: 19, 20

DESCRIPTION: Medium to large, smooth, biconvex shell displaying numerous faint growth-lines; shell ovate to elliptical, the valves fairly compressed; cardinal margin gently curved; anterior commissure weakly unisulcate. Beak somewhat produced, obtuse, almost erect, attrite; large circular mesothyrid foramen; beak ridges well defined; gently convex cardinal area with conjunct deltidial plates; fairly prominent ventral palintrope. Median septum relatively thickened, extending anteriorly about one-third of valve length, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped hinge-trough with steeply inclined walls; crural bases fused to the thickened inner socket ridges. Cardinal process consisting of roughened myophore is usually small and pyramidal, confined to the posterior portion of the hinge-trough, often developing a boss-like anterior swelling with growth that projects ventrally; the cardinal process occupies the posterior one-third of the hinge-trough, sometimes tapering anteriorly to occupy up to one-half of the hinge-trough; wing-like projections of myophore develop posteriorly. Dorsal adductor muscle scars are large and distinct, terminating anteriorly at approximately the termination point of the median septum – at one-third the length of the valve. The muscle-field scars of the ventral valve are faint, the low median ridge in the valve floor between the diductor muscle scars hard to discern. The teeth are large and sturdy, and are perched on swollen bases, which are grooved to accommodate the swollen inner socket ridges. Adult loop trabecular, the transverse connecting band attenuated.

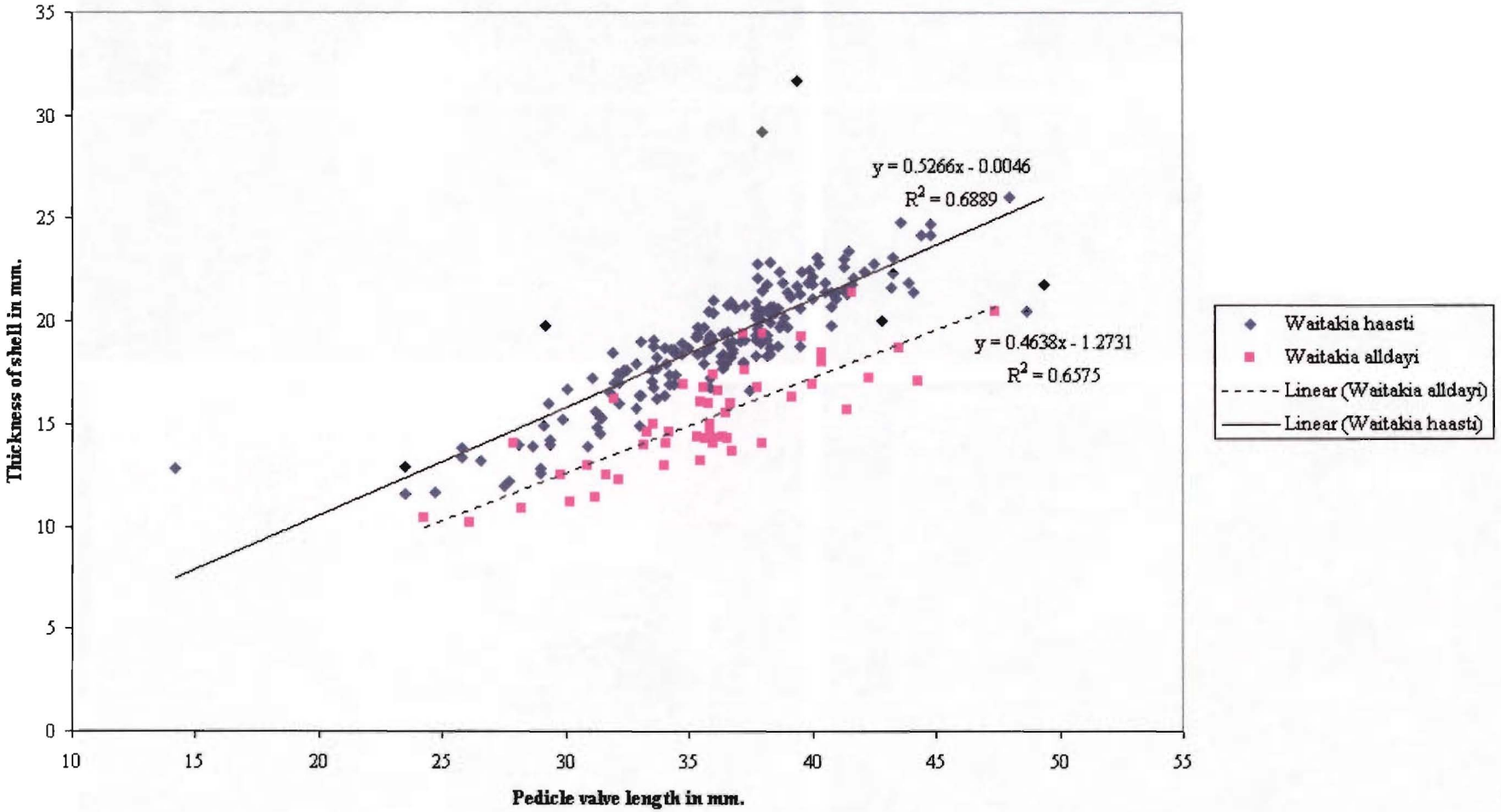
DISCUSSION: Graph 1 displays a histogram of length for *Waitakia alldayi*, while graph 2 illustrates the difference in valve inflation between *Waitakia haasti* (section 3.8) and *alldayi*. The compressed nature of *alldayi* is one of its most characteristic features, the shell externally resembling *W. haasti* in most other respects. Thomson (1920, 1926) recorded *Pachymagas marshalli* (*Waitakia marshalli* of this study) as occurring at All Day Bay and Kakanui because material from the type locality of *P. marshalli*, Milburn Quarry, displays a similarity both in characters of the beak and compressed nature to that at these localities. However, *Waitakia marshalli* occurring at Milburn Quarry is considered an ecophenotypic form in this study (section 3.9), the material from All Day Bay and Kakanui being distinctly different from *Waitakia marshalli* when taken as a whole.

It was noted that interiorly the material from Gee's Point and Kakanui was in some ways less developed than that at All Day Bay. At Gee's Point and Kakanui the median septum was observed in some species to be rather slender, not typically thickened as at All Day Bay. In addition, the cardinal process seemed to be consistently more primitive, the hinge-trough often with shallowly inclined walls. In balance to these statements, it must be noted that these observations were made mainly of material from Gee's Point. Fossils are sparsely distributed throughout the basal portion of the Waitakian greensand at Gee's Point, and the material examined tended to be smaller than that seen at All Day Bay – the specimens examined may not have reached their full size and level of development, hence the observed underdeveloped interior characters. In addition, the material from Gee's Point and Kakanui seems to represent a time when *Waitakia* was reoccupying calcareous greensands, after its excursion into limestone-forming environments during the

Graph 1: Histogram of pedicle valve length for Waitakia alldayi from All Day Bay



Graph 2: Pedicle valve length vs. Thickness for Waitakia haasti and Waitakia alldayi



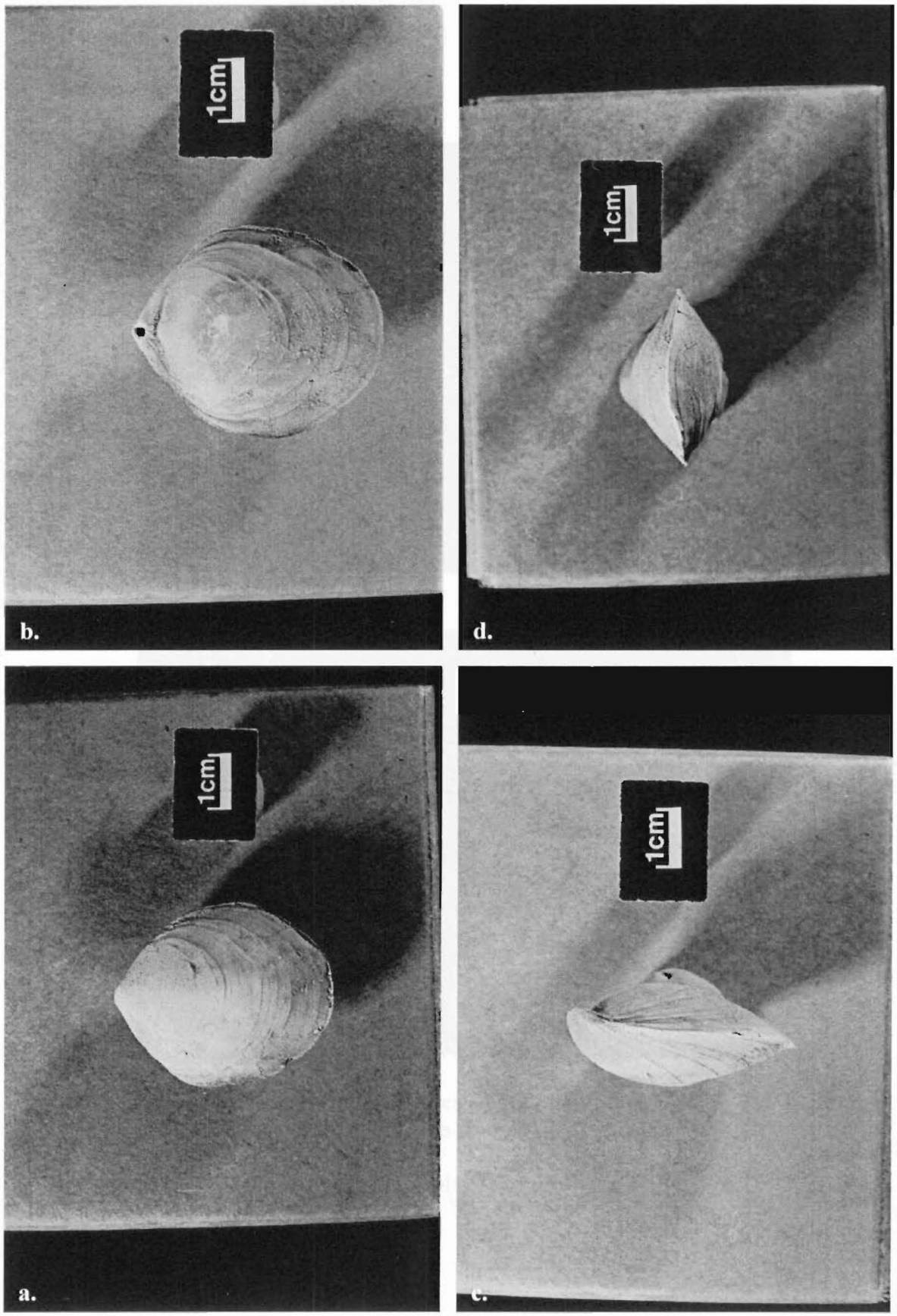


Figure 19. Holotype of *Waitakia alldayi* (Allan Colln. 26735).

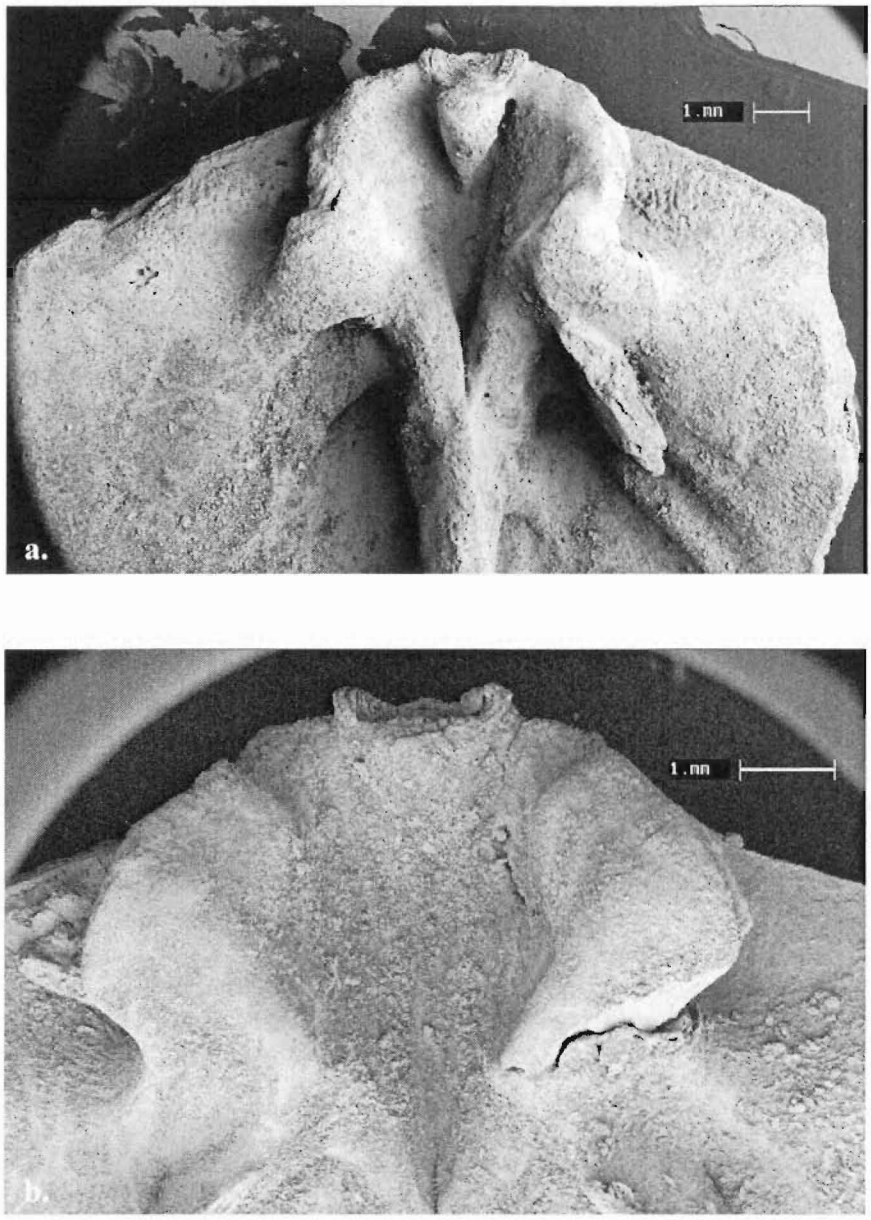


Figure 20. Dorsal interiors for paratypes of *Waitakia alldayi* (**a**: UCM 2008; **b**: UCM 2009). Both specimens from All Day Bay.

not mentions as a paratype
a p. 76.

Waitakian, and perhaps represents an early form not yet fully re-adapted to the environment; the Gee's Point material, at least, may represent a place in time where speciation was occurring. What is certain, however, is the fact that at All Day Bay *W. alldayi* occurs in a calcareous greensand with a high mud content (fig. 18); the Gee Greensand at Gee's Point and Kakanui are not muddy. There is therefore a possibility that the observed slight morphological differences are due to ecophenotypic response. Others might chose to interpret the morphological differences, if they exist outside the realms of poor sampling, as indicative of separate species, but it is felt that it is better to assign all of the material to *Waitakia alldayi* on the basis of the information at hand.

3.4 *Waitakia andrewi* (Thomson, 1920)

SYNONYMY:
Pachymagas andrewi Thomson, 1920, p. 380, pl. XXVI, figs. 1-2
"*Pachymagas*" *andrewi* Allan, 1960, p. 247, 263 (stratigraphic range)
Pachymagas andrewi Levy, 1961, p. 82, 83, 84
Pachymagas andrewi Keyes, 1971, p. 81
"*Pachymagas*" *andrewi* Dawson, 1990a, p. 62

TYPE LOCALITY: "Creamy calcareous sandstone immediately succeeding the main Mount Brown limestone, foot of the dip-slope of the latter, Weka Pass" (Thomson 1920). Calcareous sands at the base of the Glenmark Limestone Member of the Mt Brown Formation, Weka Pass, North Canterbury.

TYPE MATERIAL: Holotype (Br 120) in the National Museum of New Zealand, Wellington.

(Source: Dawson 1990a)

OCCURRENCE: Sandstones, (base of) Glenmark Limestone Member {North Canterbury}, at: Weka Pass.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (28473, 28476, 28480-28482 Weka Pass) ; (28584, 28586, 28588, 28590 Weka Pass) ; (28600-28604, 28606 Weka Pass).

AGE/RANGE: Altonian

FIGURES: 21, 22

DESCRIPTION: Medium to large, smooth, biconvex shell displaying numerous faint growth-lines; shell broadly ovate; wide cardinal margin gently curved, almost straight; anterior commissure weakly to moderately broadly unisulcate. Beak obtuse; suberect to erect, attrite; small to medium sized circular mesothyrid foramen; beak ridges well defined, bounding high ventral palintrope; gently convex cardinal area with high symphytium. Median septum relatively thickened, extending anteriorly approximately one-third of valve length, bifurcating posteriorly to unite with the hinge-plates forming a v-shaped hinge-trough with steeply inclined walls; crural bases fused to the thickened inner socket ridges. Cardinal process consisting of roughened myophore and very large bulbous anterior swelling occupies three-quarters of the hinge-trough; wing-like projections of myophore develop posteriorly. Adult loop trabecular?

DISCUSSION: The interior characteristics of the species are here described from examination of but three specimens: the holotype (Br 120), which has been partially excavated from the ventral side, and two specimens from the Allan Collection (28586, 28588) which were partially excavated with the aid of an air-scribe. None of the interiors of theses specimens are suitable for photography, and as such cannot be illustrated. The cardinalia, as far as can be determined from the three excavated specimens, resembles that of *W. bartrumi*, so the reader is referred to the illustrations of the interior for that species (figs. 37a, b, c ; 38a, b). Thomson (1920) remarked that the species could conceivably belong to the genus *Neothyris*, though his holotype (Br 120) has been partially excavated from the ventral side, presumably by Thomson himself, and seems to display a remnant of a connecting band, though this could easily be secondary calcite adhering to the septum. Allan Collection specimen 28586 was partially excavated during this study, and appears to display remnants of a connecting band, so it is considered that *andrewi* possessed a trabecular loop, and should be placed in the genus *Waitakia* rather than *Neothyris*.

The species is rather distinctive in its exterior shape and, as Thomson (1920) noted, its possession of a small foramen. It was however determined that the size of the foramen does vary somewhat, being of moderate size in some specimens, but does typically seem to be smaller than for most species of this genus. The species occurs in association with *Neothyris* (?) *anceps* Thomson in the creamy calcareous sandstone (fig. 11), and throughout the sandstones and associated minor shellbeds below the base of the Glenmark Limestone proper (McCulloch 1981). Thomson evidently recorded the species as *Pachymagas cottoni* (*Waitakia cottoni*) in creamy limestone approximately 0.5 m above creamy sandstone in which he identified *Pachymagas*

andrewi (*Waitakia andrewi*), and as *Pachymagas huttoni* (*Waitakia marshalli*) in muddy sands some 6 m above the creamy limestone (Thomson 1920, p. 362-363). Though this record of *cottoni* and *huttoni* is thought to represent *W. andrewi* (see below), the occurrence of *cottoni* cannot be equivocally ruled out, *cottoni* therefore perhaps ranging from the "Mount Donald horizon" (Allan 1937c) into the Altonian sands above the main "Rhizothyris-Pachymagas bed" (Fleming 1963).

Waitakia andrewi seems to vary substantially in external shape, sometimes resembling *Waitakia cottoni* (q.v.) in outline, though being less convex and having a relatively narrower cardinal margin (figs. 21a ; 22a, d). The few specimens that were available for study seemed to demonstrate that, where the species possesses a suberect beak, the beak has invariably suffered more attrition than for those specimens with an erect beak. Specimens displaying suberect beaks are usually more suborbicular in outline than those without such beaks (fig. 22d). There seems to be gradation between the two morphs. While the more suborbicular morphs may perhaps represent forerunners, or earliest representatives, of the species, not yet fully adapted to the environment, it is considered likely that these forms represent individuals that found attachment on surfaces sufficiently large enough to allow the pedicle to be actively used in the adult. Specimens with small foramens and erect beaks probably found juvenile attachment on surfaces that didn't lend themselves to support of the adult, the pedicle not actively used. In support of the latter hypothesis is the apparent co-occurrence of the two morphs at various horizons in the sands at the base of the Glenmark Limestone Member, though the relevant records of the Allan Collection are less than sufficient for establishing exact stratigraphic occurrence in this instance. The

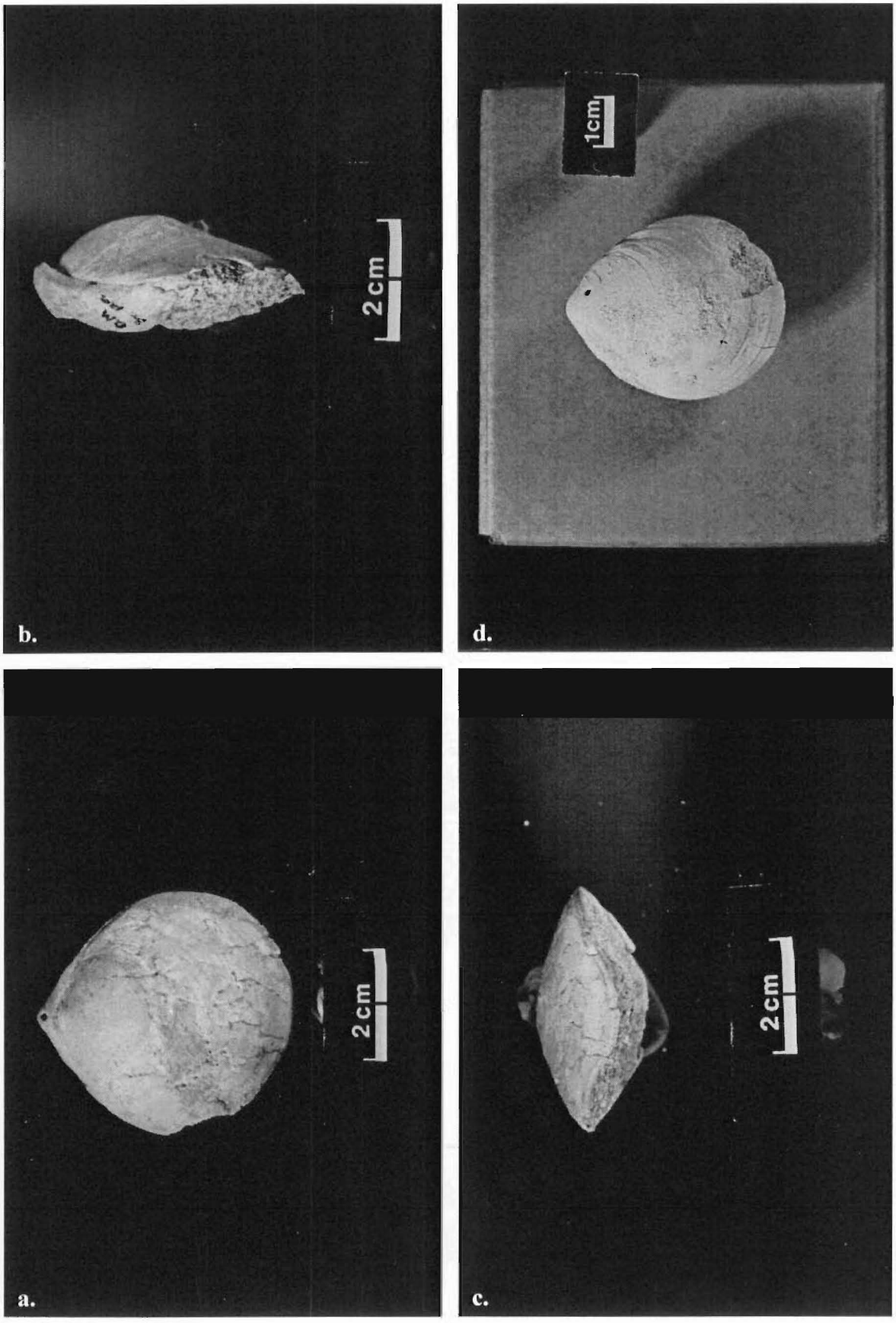


Figure 21. Holotype (**a**, **b**, **c**: Br 120) of *Pachymagas andrewi* and ventral exterior of *Waitakia andrewi* (**d**: Allan Colln. 28481; from Weka Pass).

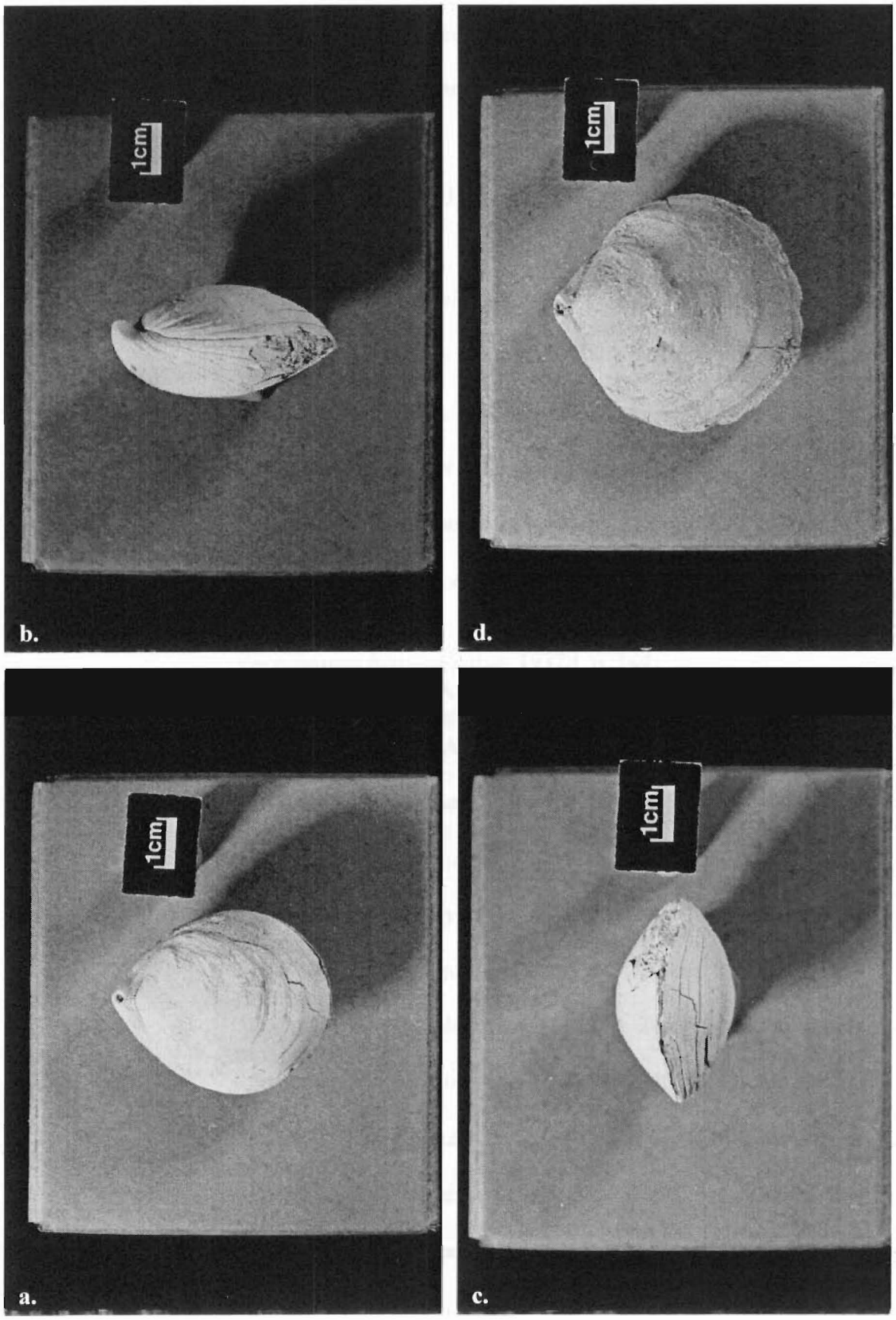


Figure 22. *Waitakia andrewi* (**a**, **b**, **c**: Allan Colln. 28481; **d**: Allan Colln. 28604) from Weka Pass.

species possibly evolved from *Waitakia cottoni*, the more suborbicular morphs of *andrewi* resembling their ancestor in exterior shell shape and (hence?) habit.

3.5 *Waitakia bartrumi* (Thomson, 1920)

SYNONYMY:

Pachymagas bartrumi Thomson, 1920, p. 376, pl. XXIV, figs. 7-9
Pachymagas speighti Thomson, 1920, p. 376, pl. XXV, figs. 12-14
Pachymagas mckayi Thomson, 1920, p. 378-379, pl. XXVII, figs. 1-3
Pachymagas morgani Thomson, 1920, p. 379, pl. XXVII, figs. 4-6
Pachymagas coxi Thomson, 1920, p. 379, pl. XXVI, figs. 10-12
Pachymagas bensoni Allan, 1937b, p. 129, pl. XVII, figs. 1-3
Pachymagas forbesi Allan, 1937c (in part), p. 134-135, pl. XVIII, figs. 1-2
Pachymagas bensoni Allan, 1937d, p. 144
Pachymagas finlayi Allan, 1937d, p. 145, pl. XIX, figs. 1-2
Pachymagas mcdowalli Allan, 1937d, p. 146, pl. XIX, figs. 3-4
Pachymagas ulrichi Allan, 1937d, p. 146-147, pl. XIX, figs. 5-6
"*Pachymagas*" *bartrumi* Allan, 1960, p. 245, 263 (stratigraphic range)
"*Pachymagas*" *coxi* Allan, 1960, p. 245, 263 (stratigraphic range)
"*Pachymagas*" *mckayi* Allan, 1960, p. 245, 264 (stratigraphic range)
"*Pachymagas*" *morgani* Allan, 1960 (in part), p. 245, 264 (stratigraphic range)
"*Pachymagas*" *speighti* Allan, 1960, p. 245, 264 (stratigraphic range)
"*Pachymagas*" *bensoni* Allan, 1960, p. 245, 263 (stratigraphic range)
"*Pachymagas*" *finlayi* Allan, 1960, p. 246, 263 (stratigraphic range)
"*Pachymagas*" *mcdowalli* Allan, 1960, p. 246, 264 (stratigraphic range)
"*Pachymagas*" *forbesi* Allan, 1960, p. 246, 263 (stratigraphic range)
"*Pachymagas*" *ulrichi* Allan, 1960, p. 252, 265 (stratigraphic range)
Pachymagas bartrumi Keyes, 1971, p. 81
Pachymagas coxi Keyes, 1971, p. 82
Pachymagas mckayi Keyes, 1971, p. 82

Pachymagas morgani Keyes, 1971, p. 82
Pachymagas speighti Keyes, 1971, p. 82
"*Pachymagas*" *bartrumi* Dawson, 1990a, p. 62-63
"*Pachymagas*" *bensoni* Dawson, 1990a, p. 63
"*Pachymagas*" *coxi* Dawson, 1990a, p. 64-65
"*Pachymagas*" *finlayi* Dawson, 1990a, p. 65
"*Pachymagas*" *forbesi* Dawson, 1990a, p. 65
"*Pachymagas*" *mcdowalli* Dawson, 1990a, p. 67
"*Pachymagas*" *mckayi* Dawson, 1990a, p. 67-68
"*Pachymagas*" *morgani* Dawson, 1990a, p. 69
"*Pachymagas*" *speighti* Dawson, 1990a, p. 70-71
"*Pachymagas*" *ulrichi* Dawson, 1990a, p. 72

TYPE LOCALITY: "Foot of dip-slope, main Mount Brown limestone, Weka Pass" (Thomson 1920). "Rhizothyris-Pachymagas bed" (Fleming 1963 and see fig. 11) at top of upper 'lens' (Browne & Field 1985) of the Main Mt Brown Limestone Member of the Mount Brown Formation, Weka Pass, North Canterbury.

TYPE MATERIAL: Holotype (Br 126) in the National Museum of New Zealand, Wellington. Holotypes of *Pachymagas coxi* (Br 1340), *Pachymagas mckayi* (Br 123), *Pachymagas morgani* (Br 121), and *Pachymagas speighti* (Br 122) in the National Museum of New Zealand, Wellington. Holotypes of *Pachymagas bensoni* (UCM 1465/Allan Colln. No. 958), *Pachymagas finlayi* (UCM 1472/Allan Colln. No. 1818), *Pachymagas mcdowalli* (UCM 1471/Allan Colln. No. 1817), *Pachymagas ulrichi* (UCM 1468/Allan Colln. No. 1394), and *Pachymagas forbesi* (UCM 1469/Allan Colln. No. 1478) plus paratype (UCM 1470/Allan Colln. No. 1480) in the Department of Geological Sciences, University of Canterbury, Christchurch. Paratype (B3) of *Pachymagas speighti* in Canterbury Museum, Christchurch.

(Source: Dawson 1990a)

OCCURRENCE: Main Mt Brown Limestone {North Canterbury}, at: Weka Pass; Sharks Tooth Hill and Woody Knoll Members of the Forest Hill Formation {Southland}, at: Clifden, Clifden Quarry, Doherty's Quarry, Fernhill Quarry, Lady Barkly Quarry, Forest Hill Quarry, Ward's Quarry, Centre Bush, Limehills; Otahu Formation {Southland}, at: Clifden; Nga Pari Formation {Southland}, at: Clifden.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (651-791 Weka Pass) ; (853-967 Weka Pass) ; (2242-2380 Weka Pass) ; (26206, 26207, 26212-26221 Clifden) ; (26242-26262 Clifden) ; (26263-26415 Clifden) ; (29093-29254 Clifden) ; (1266-1286 Doherty's Quarry) ; (1330-1373 Doherty's Quarry) ; (26429-26458 Doherty's Quarry) ; (29255-29487 Doherty's Quarry) ; (1288, 1290, 1291, 1310, 1313, 1325, 1326 Ward's Quarry) ; (1374-1404 Ward's Quarry) ; (26615-26635 Ward's Quarry) ; (26486, 26488, 26489 Forest Hill Quarry) ; (29488-29553 Forest Hill Quarry) ; (28878-29092 Fern Hill Quarry). Unnumbered collections, University of Canterbury: (Ward's Quarry (tray), Clifden Quarry (3 bags), Clifden (bag), Weka Pass (2 bags): D. I. MacKinnon Collection) ; (Weka Pass (4 bags): S. Fryer MSc. Thesis Collection).

AGE/RANGE: Altonian-Clifdenian?

FIGURES: 23-38

DECRIPTION: Medium to large, smooth, biconvex shell displaying numerous faint growth-lines; shell elliptical; cardinal margin moderately wide and curved, characteristically deflected posteriorly at the umbo; anterior commissure moderately to relatively strongly unisulcate. Beak obtuse, suberect to erect, attrite; large circular

mesothyrid foramen; beak ridges well defined, bounding prominent ventral palintrope; gently to moderately convex cardinal area with relatively high and broad symphytium or, rarely, conjunct deltidial plates. Median septum thick, extending anteriorly about one-third of valve length, bifurcating posteriorly to unite with the hinge-plates forming a v-shaped hinge-trough with steeply inclined walls; the hinge-plates, fused medially with the septum, usually becoming detached from the septum anteriorly; crural bases fused to the thickened inner socket ridges. Cardinal process consisting of roughened myophore and very large bulbous anterior swelling occupies three-quarters of the hinge-trough; wing-like projections of myophore develop posteriorly; a prominent median ridge is often displayed along the upper part of the process, either side of which the diductor muscles ran to attach posteriorly; bulbous anterior swelling projects ventrally such that grooves occur along its sides, marking the path of the dorsal pedicle adjustor muscles, which attached at the posterior of the hinge-trough. Dorsal adductor muscle scars are large and distinct, terminating anteriorly at approximately the termination point of the median septum – at one-third the length of the valve. The teeth are large and sturdy, and are perched on swollen bases, which are grooved to accommodate the swollen inner socket ridges. Adult loop trabecular, possibly transitional to teloform.

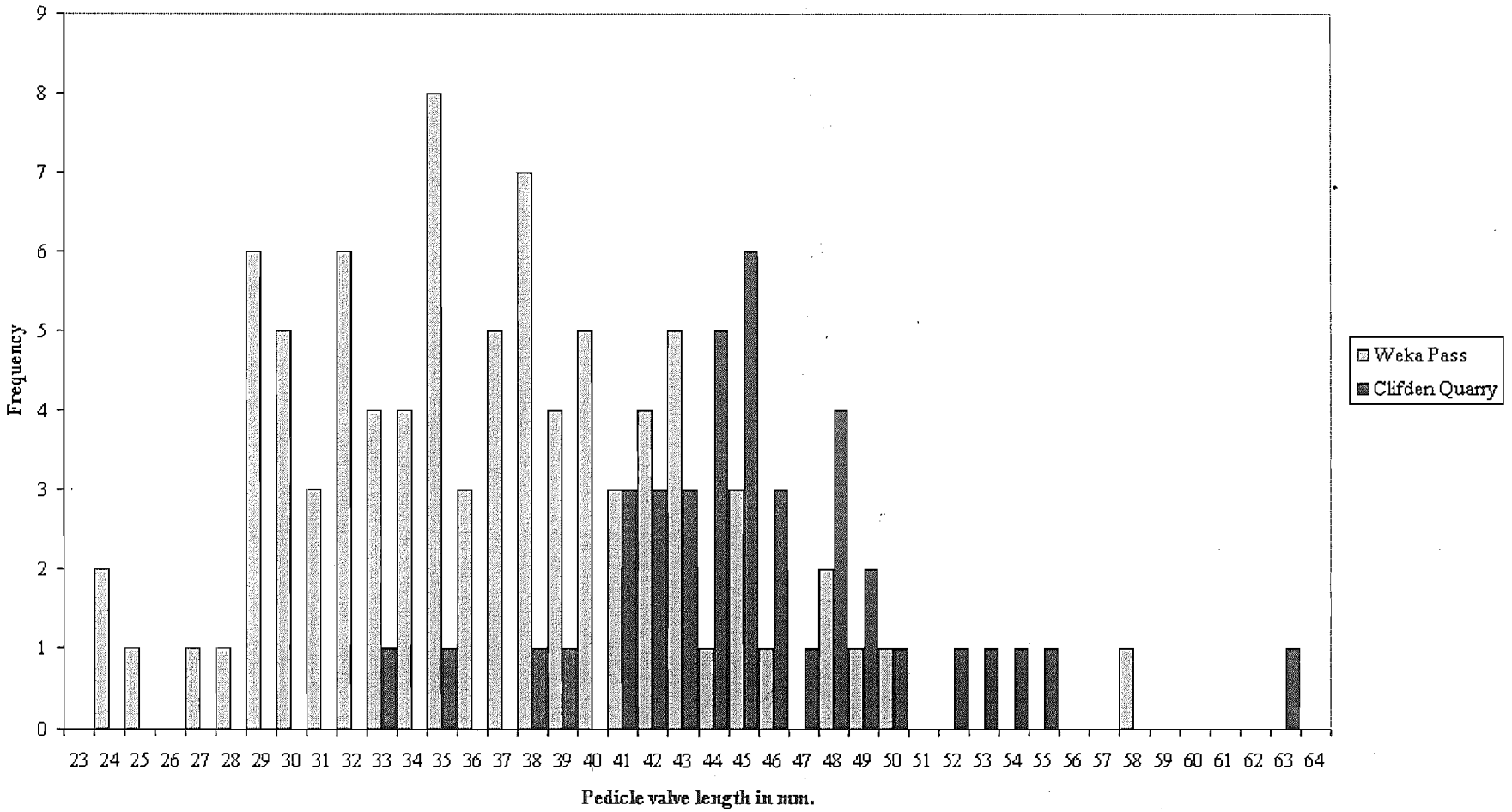
DISCUSSION: Nine species (figs. 24-32) are here synonymised with *W. bartrumi*, all of which seem to originally have been distinguished purely on minor variations in exterior shell shape. During this study, it was not found that there were distinct morphotypes amongst the brachiopod populations at Weka Pass and Clifden, the recognition of which, at least, being a prerequisite to the establishment of these species. Many of the species were originally recorded as being rare at these localities,

and this can be explained by their occurrence at the ends of the spectrum of variability for the populations – occupation of a such a position would lead to that 'species' rare occurrence in a locality.

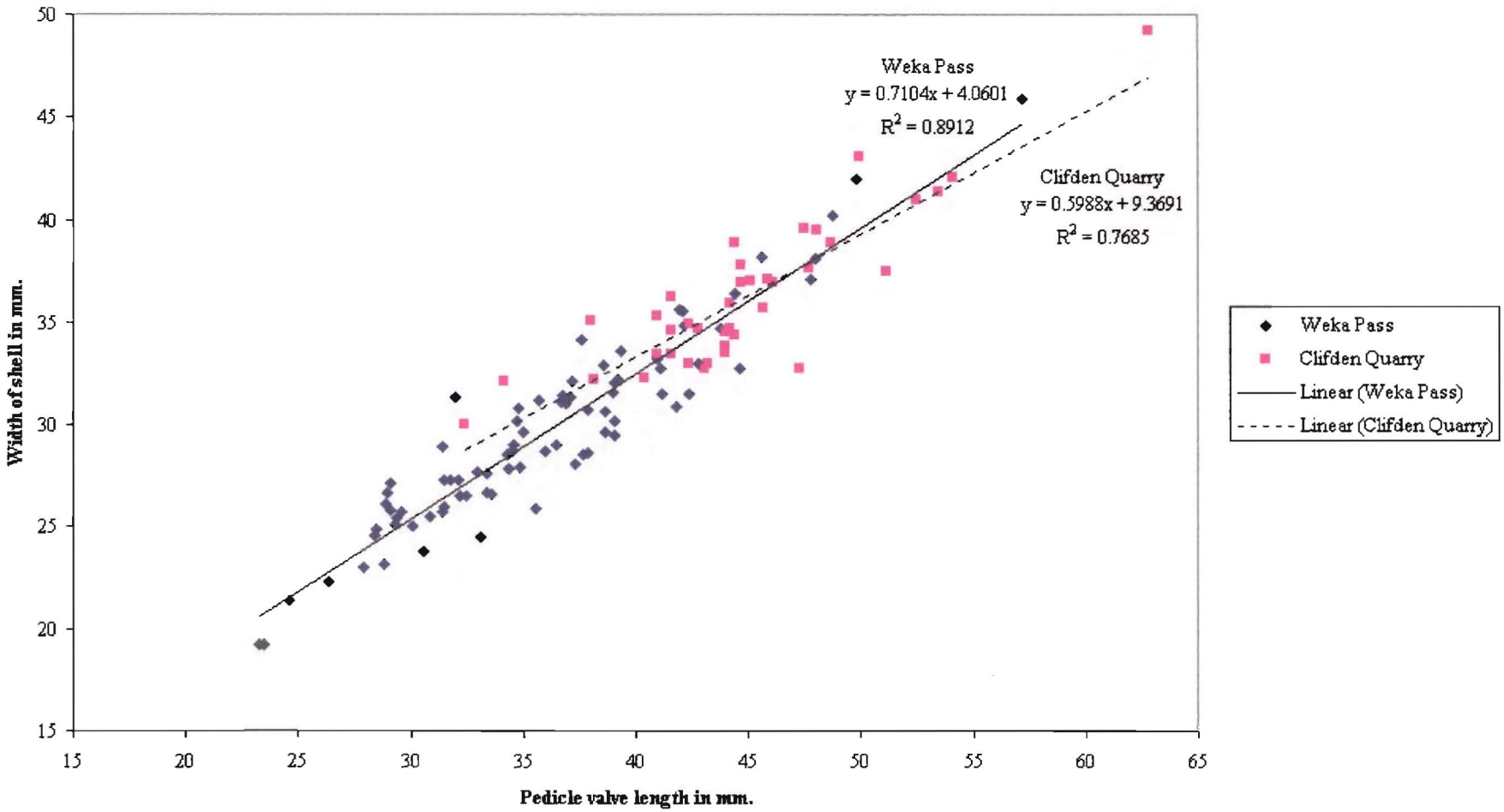
As is shown by both the histogram (graph 3) and scatter-plot (graph 4), maximum shell length of the populations from both localities is similar, but modal lengths are not, Weka Pass material being significantly smaller than that at Clifden. This can be explained by a difference in horizon between the two localities, the brachiopod horizon at Weka Pass probably older than that at Clifden. The specimens found at Weka Pass, while definitely specifically equivalent to specimens at Clifden, seem to show a greater instance of possession of erect beaks as opposed to suberect beaks. The instance of possession of conjunct deltidial plates as opposed to presence of symphytia, while not high, is higher than observed at Clifden. The cardinal process is usually larger and fills more of the hinge-trough in specimens from Clifden in comparison to specimens from Weka Pass (e.g. fig. 38). Some few excavated specimens from Clifden also demonstrate that the loop may have been at the transitional stage between trabecular and teloform; specimens from the stratigraphically higher Lillburnian Lill Sand at Clifden demonstrate possession of teloform adult loops, and were classified as *Neothyris* cf. *novara* by Fleming et al. (1969). The observed differences and their nature suggests that the species is younger at Clifden, and has evolved slightly further than at Weka Pass.

The observation that *Waitakia* is in the process of losing the connecting band, the loop in the act of passing into the teloform stage in uppermost Altonian strata (Long Beach Shellbed, Clifden), along with the observation that specimens have no connecting band and a teloform loop, necessitating reference to the genus *Neothyris*,

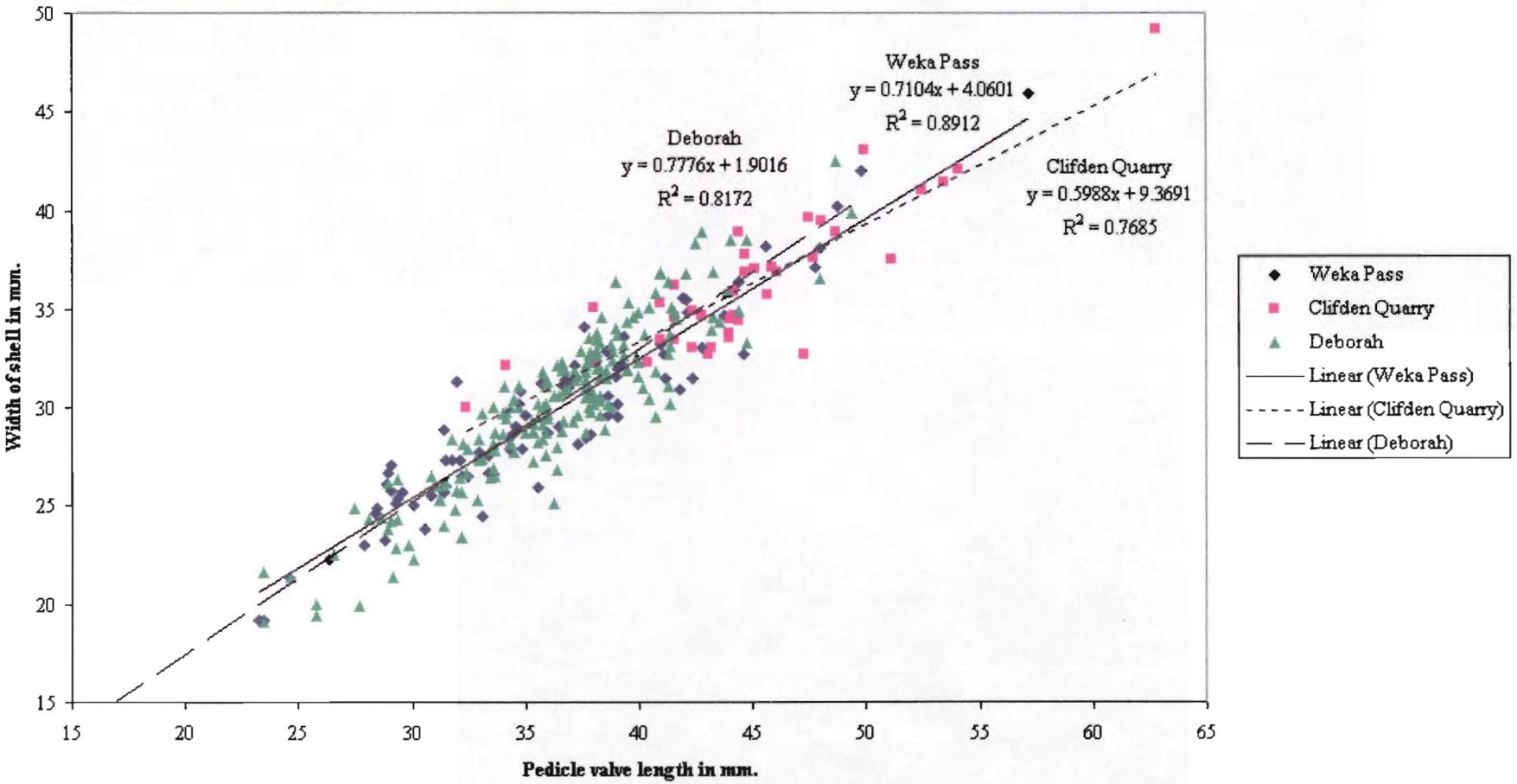
Graph 3: Histograms of pedicle valve length for Waitakia bartrumi from Weka Pass and Clifden Quarry



Graph 4: Pedicle valve length vs. Width for Waitakia bartrumi from Weka Pass and Clifden Quarry



Graph 5: Pedicle valve length vs. Width for Waitakia bartrumi from Weka Pass and Clifden Quarry, and Waitakia haasti from Deborah



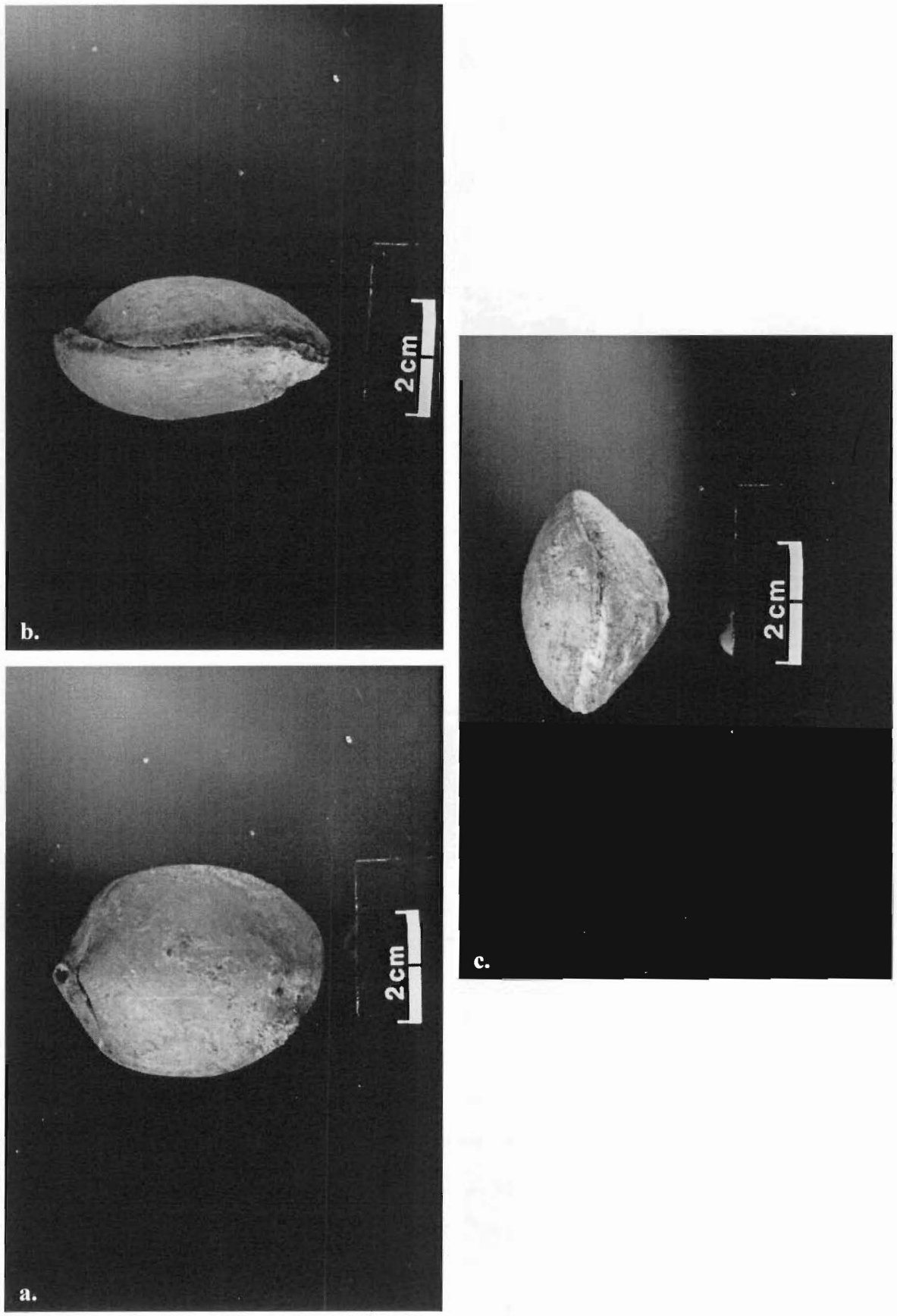


Figure 23. Holotype (Br 126) of *Pachymagas hartrumi*.

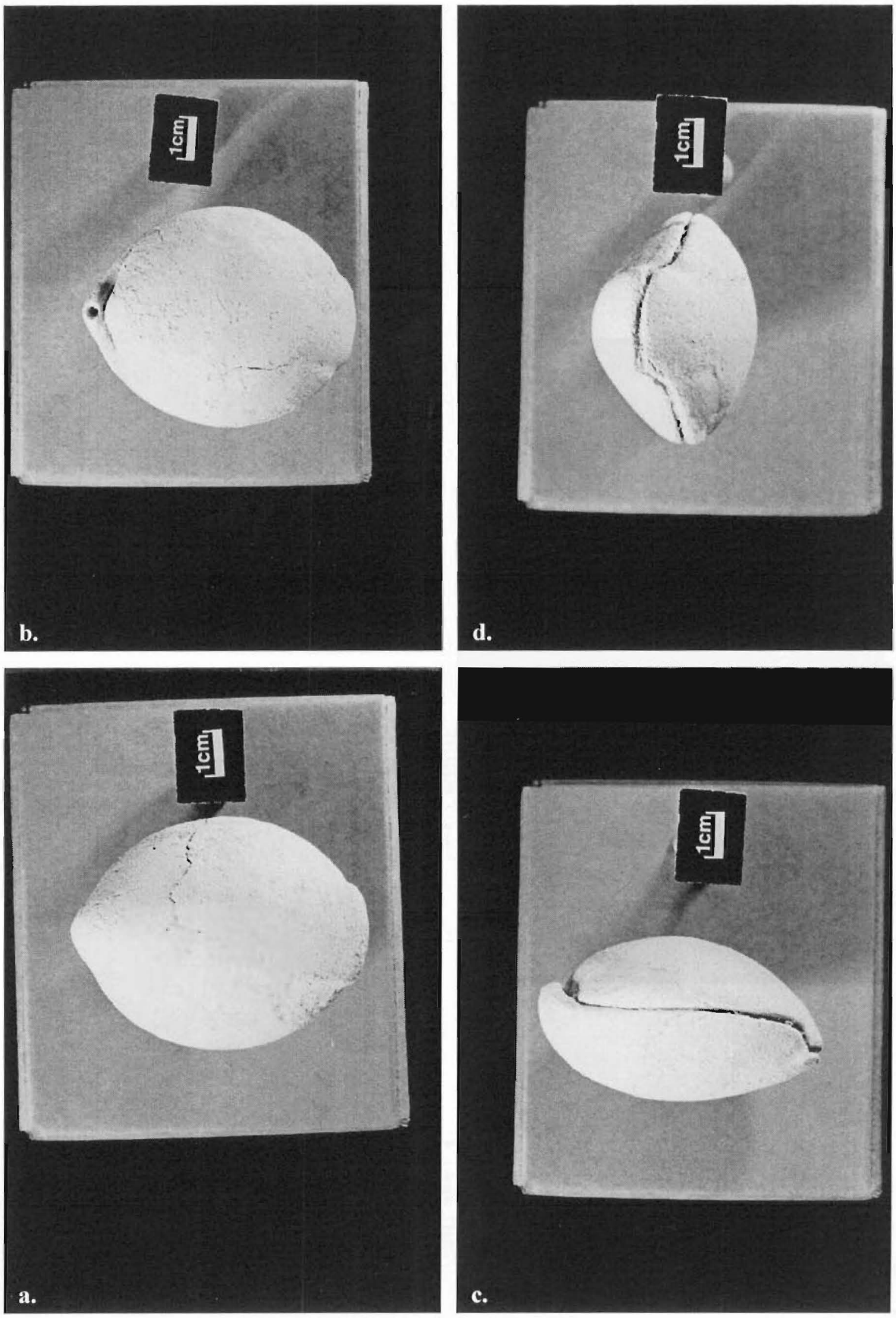


Figure 24. Holotype (UCM 1465/Allan Colln. 958) of *Pachymagas bensoni*.

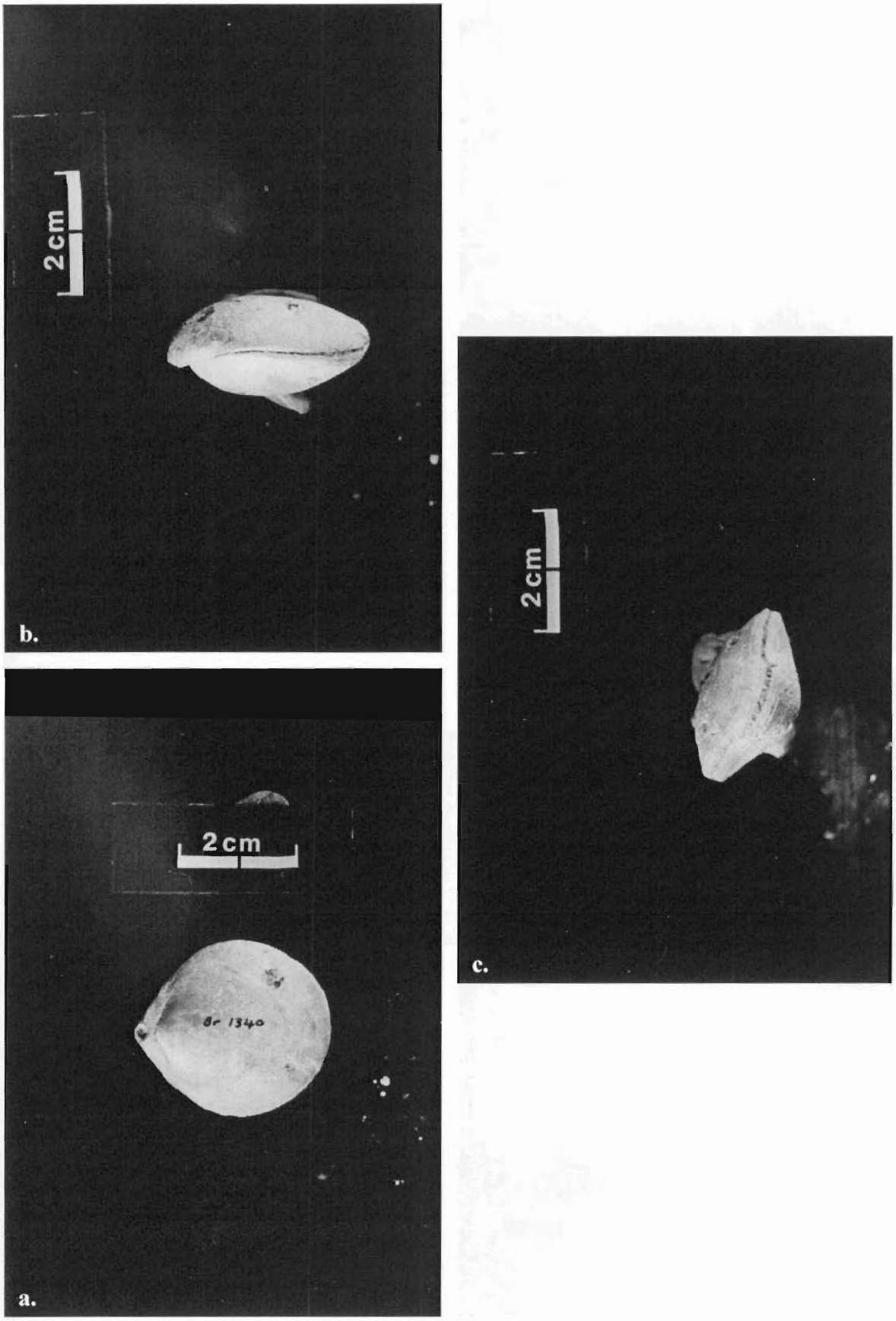


Figure 25. Holotype (Br 1340) of *Pachymagas coxi*.

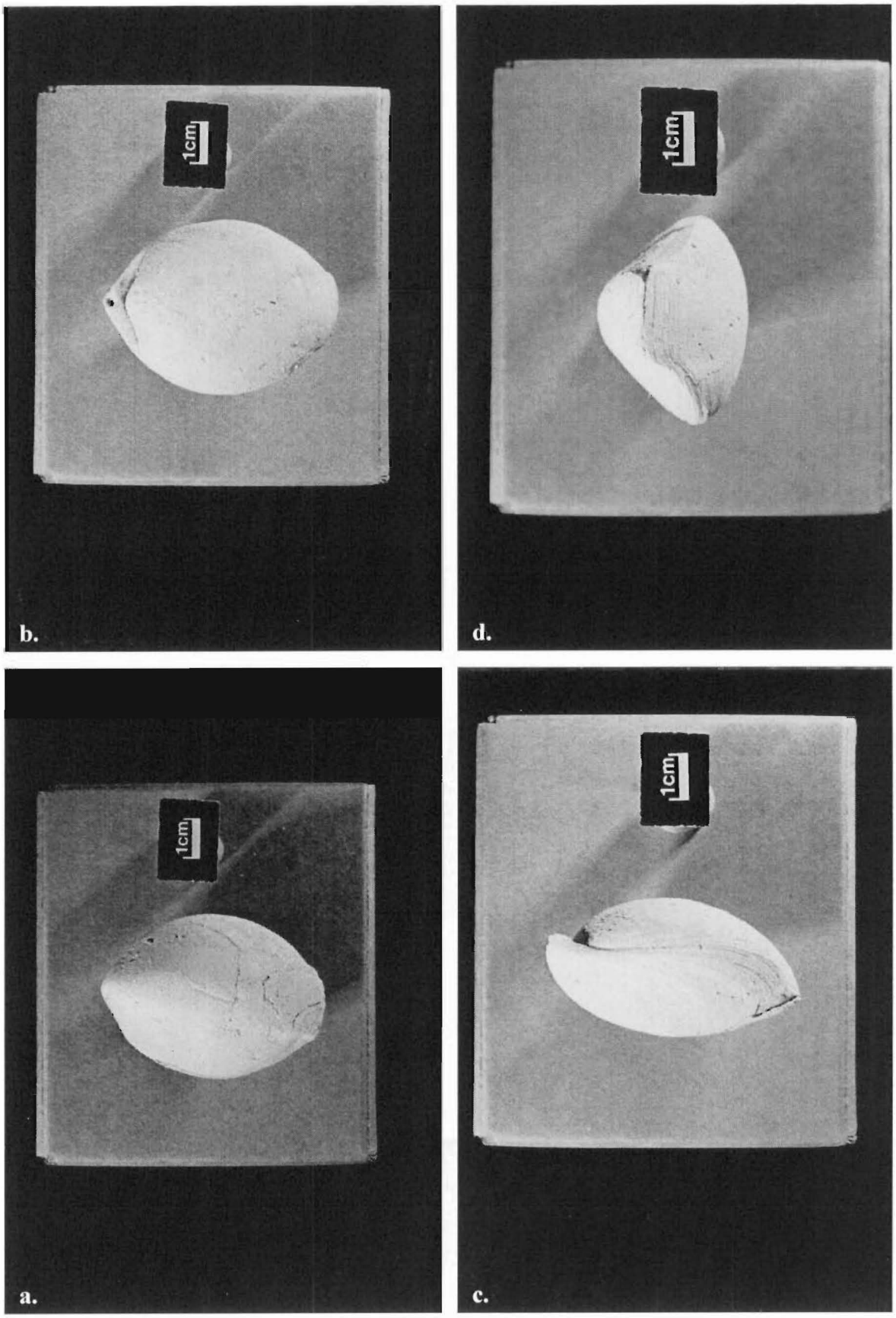


Figure 26. Holotype (UCM 1472/Allan Colln. 1818) of *Pachymagas finlayi*.

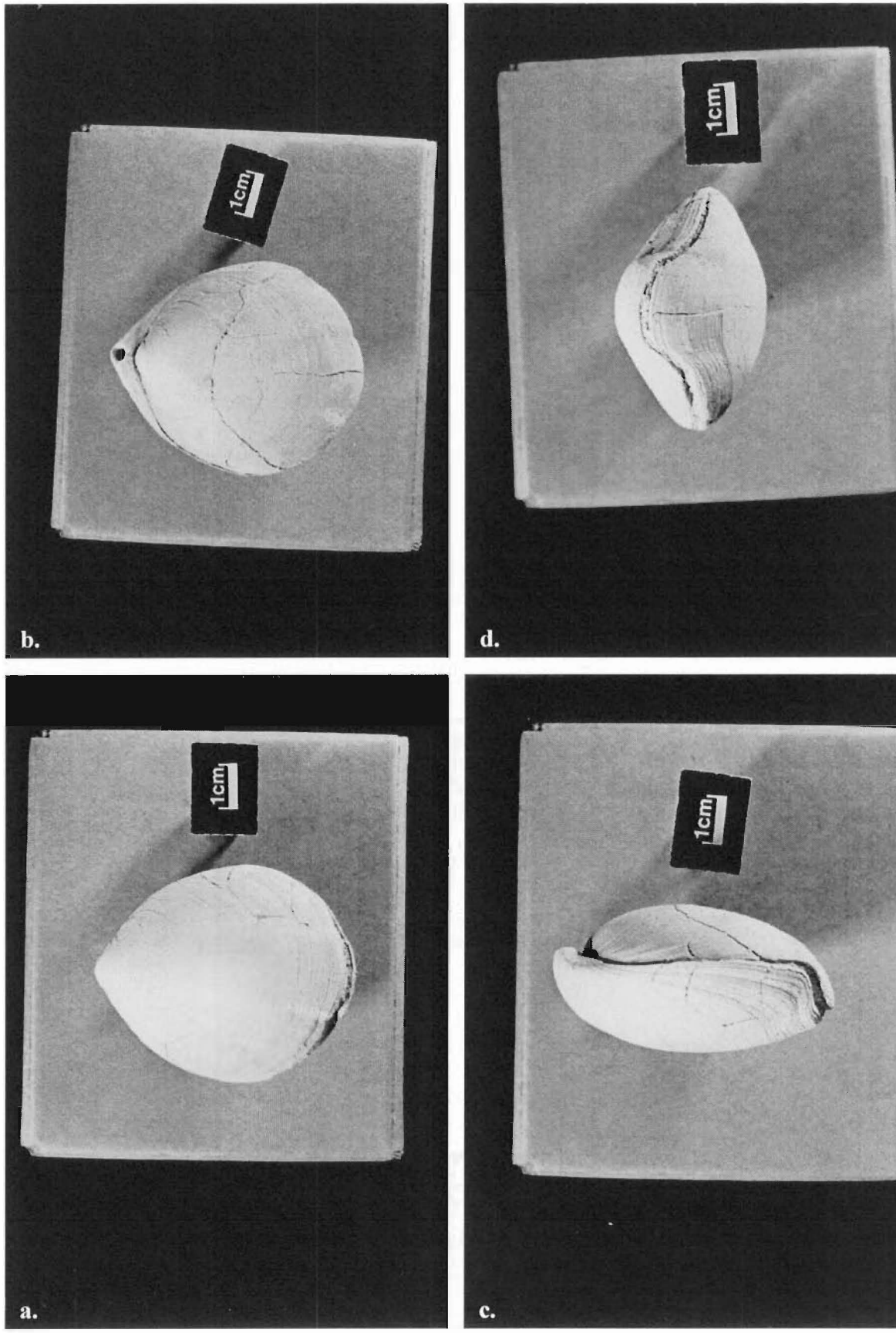


Figure 27. Holotype (UCM 1469/Allan Colln. 1480) of *Pachymagas forbesi*.

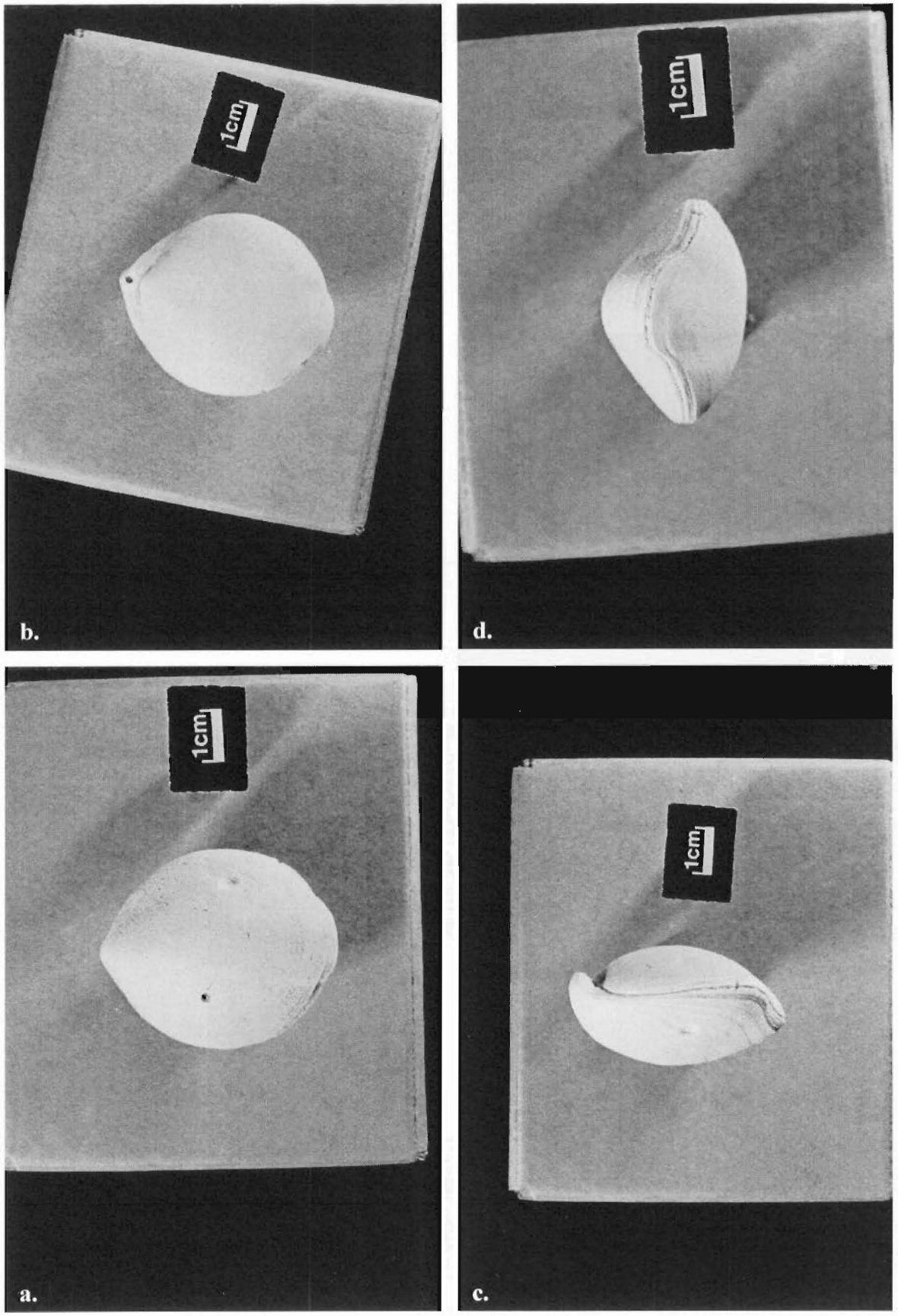


Figure 28. Holotype (UCM 1471) of *Pachymagas mcdowalli*.

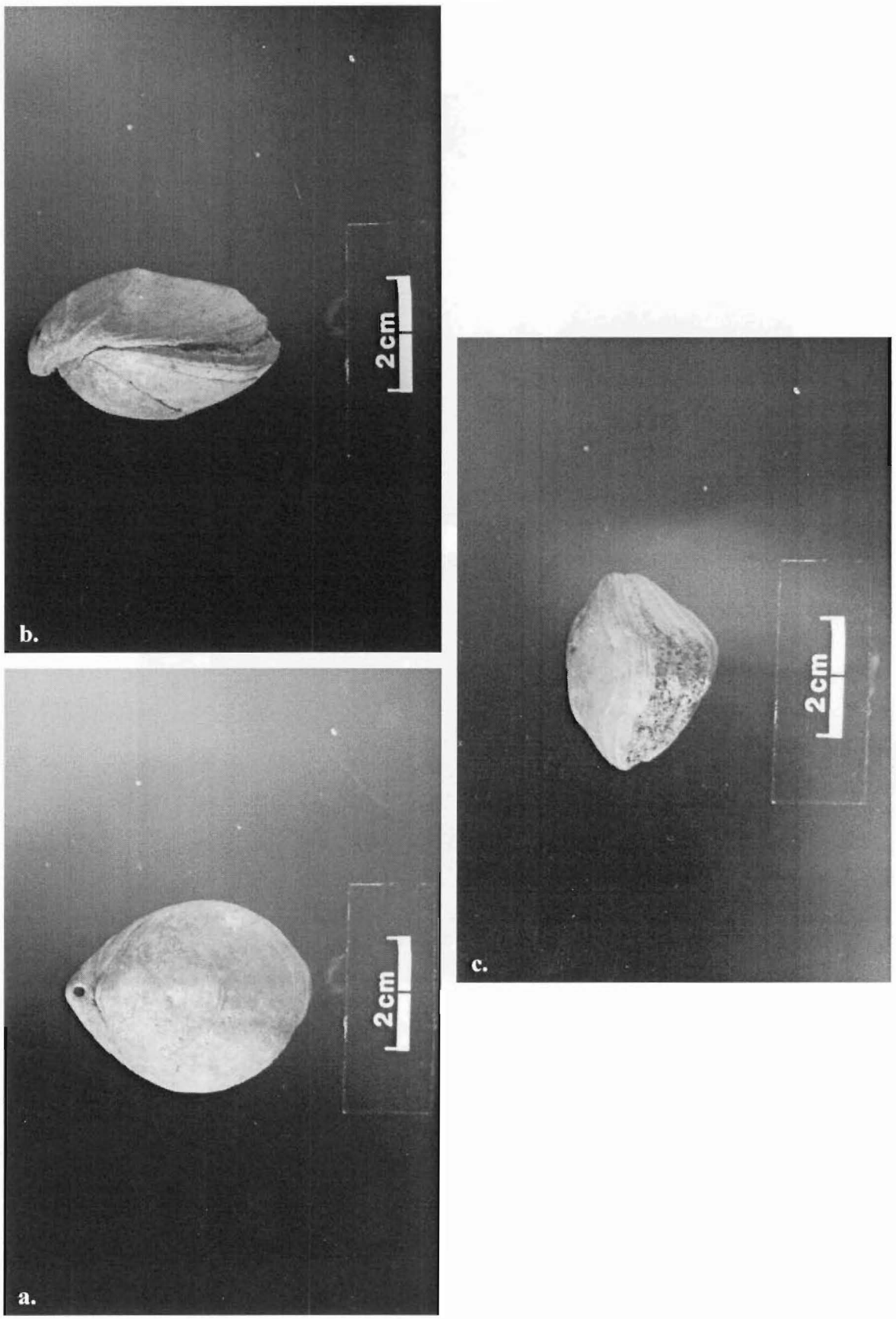


Figure 29. Holotype (Br 123) of *Pachymagas mckayi*.

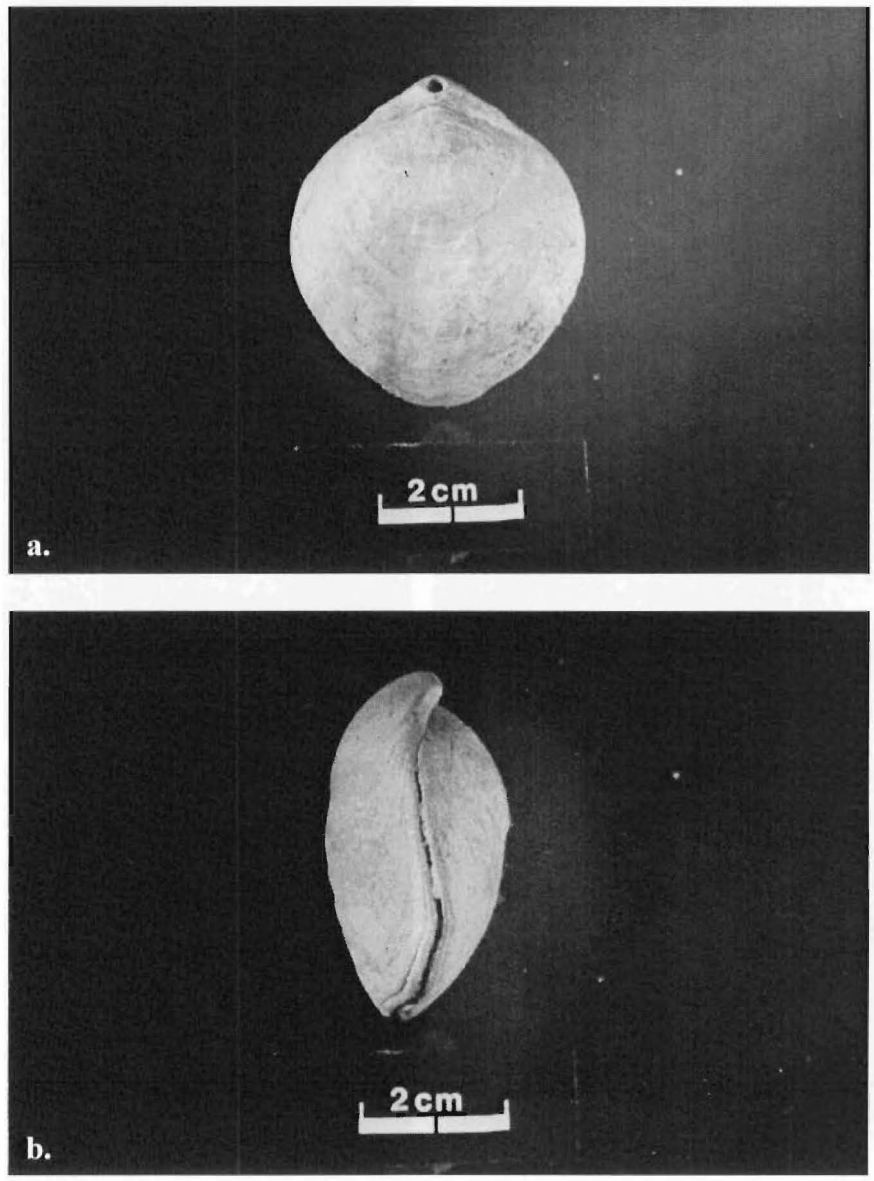


Figure 30. Holotype (Br 121) of *Pachymagas morgani*.

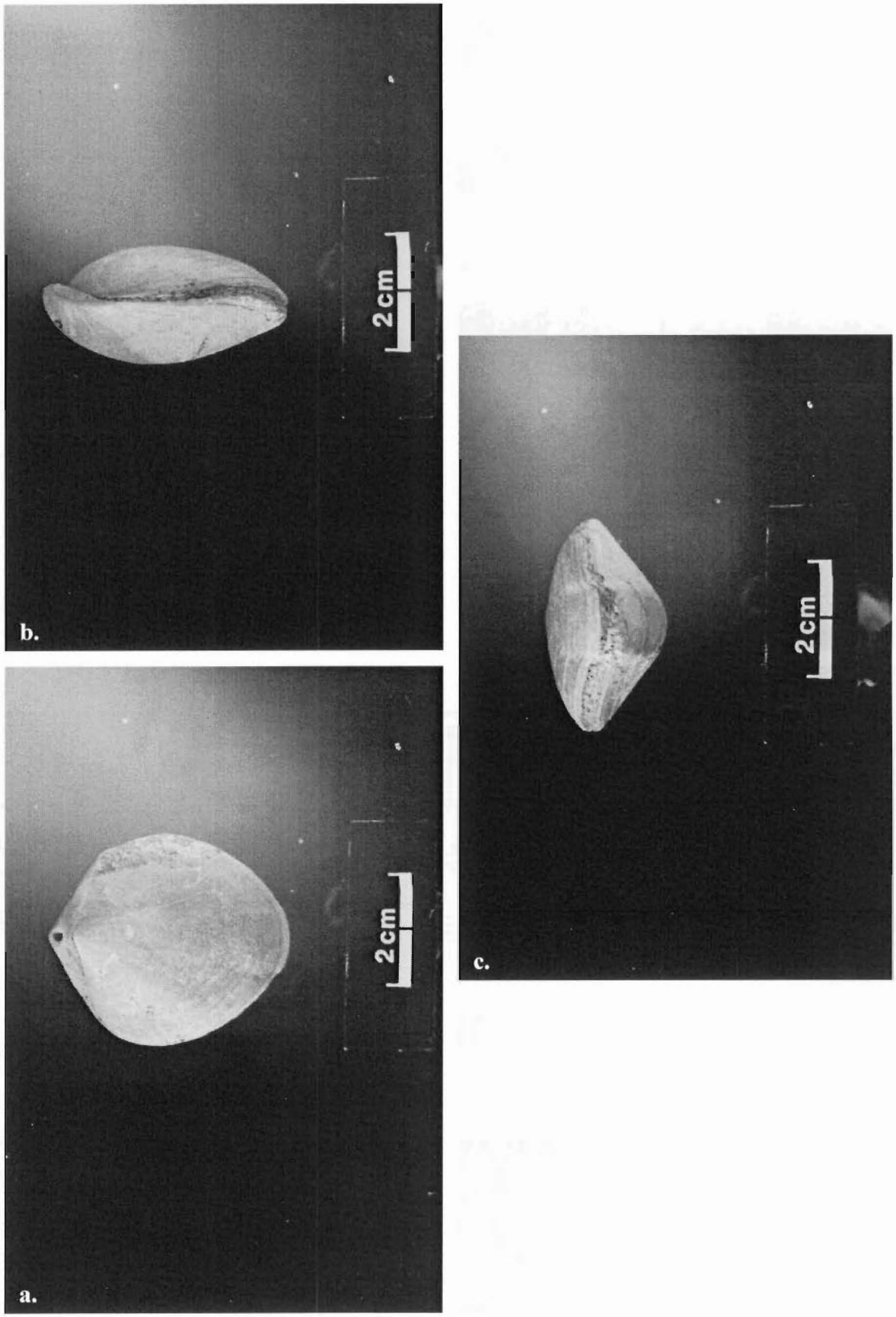


Figure 31. Holotype (Br 122) of *Pachymagas speighti*.

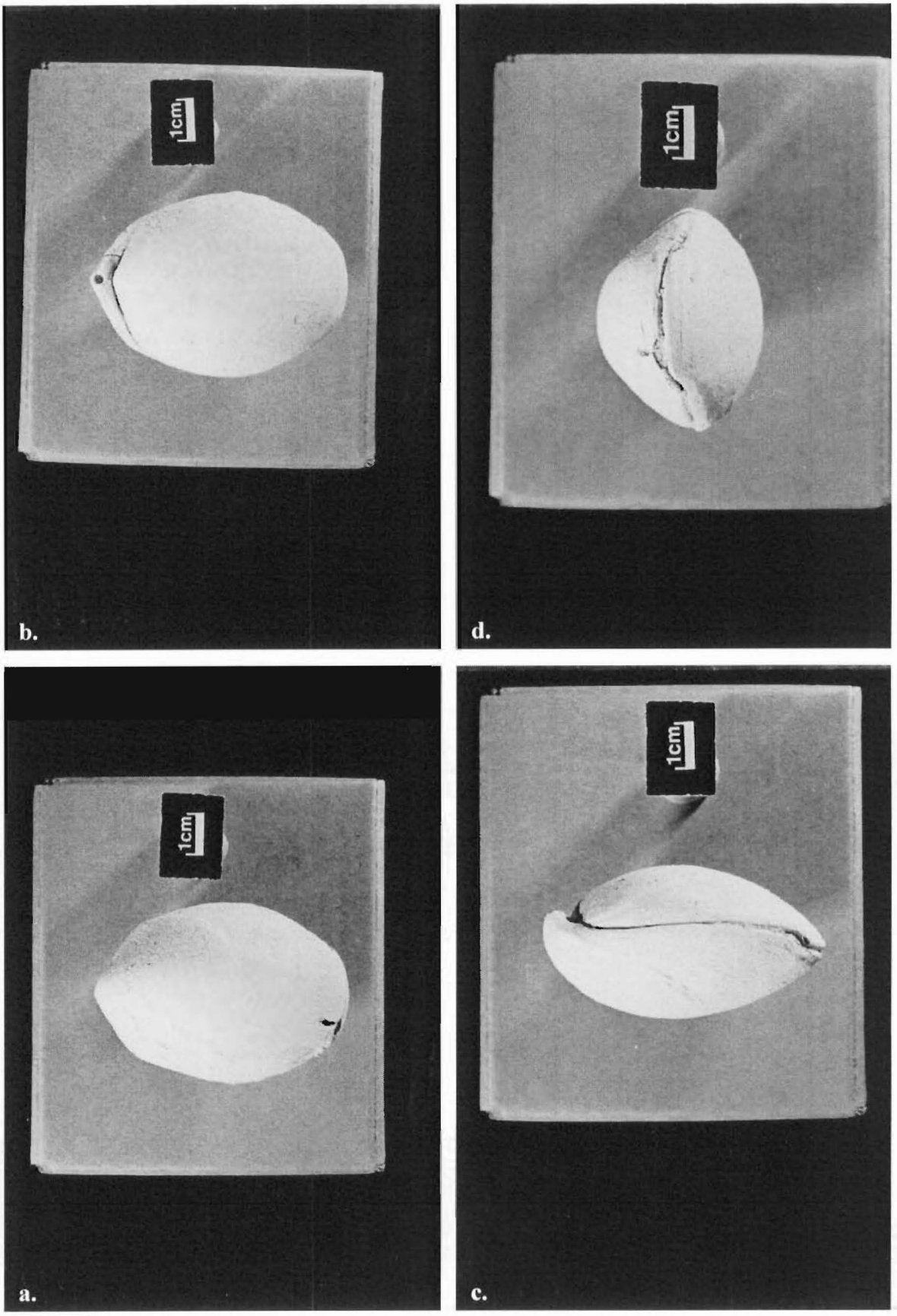


Figure 32. Holotype (UCM 1468/Allan Colln. 1394) of *Pachymagas ulrichi*.

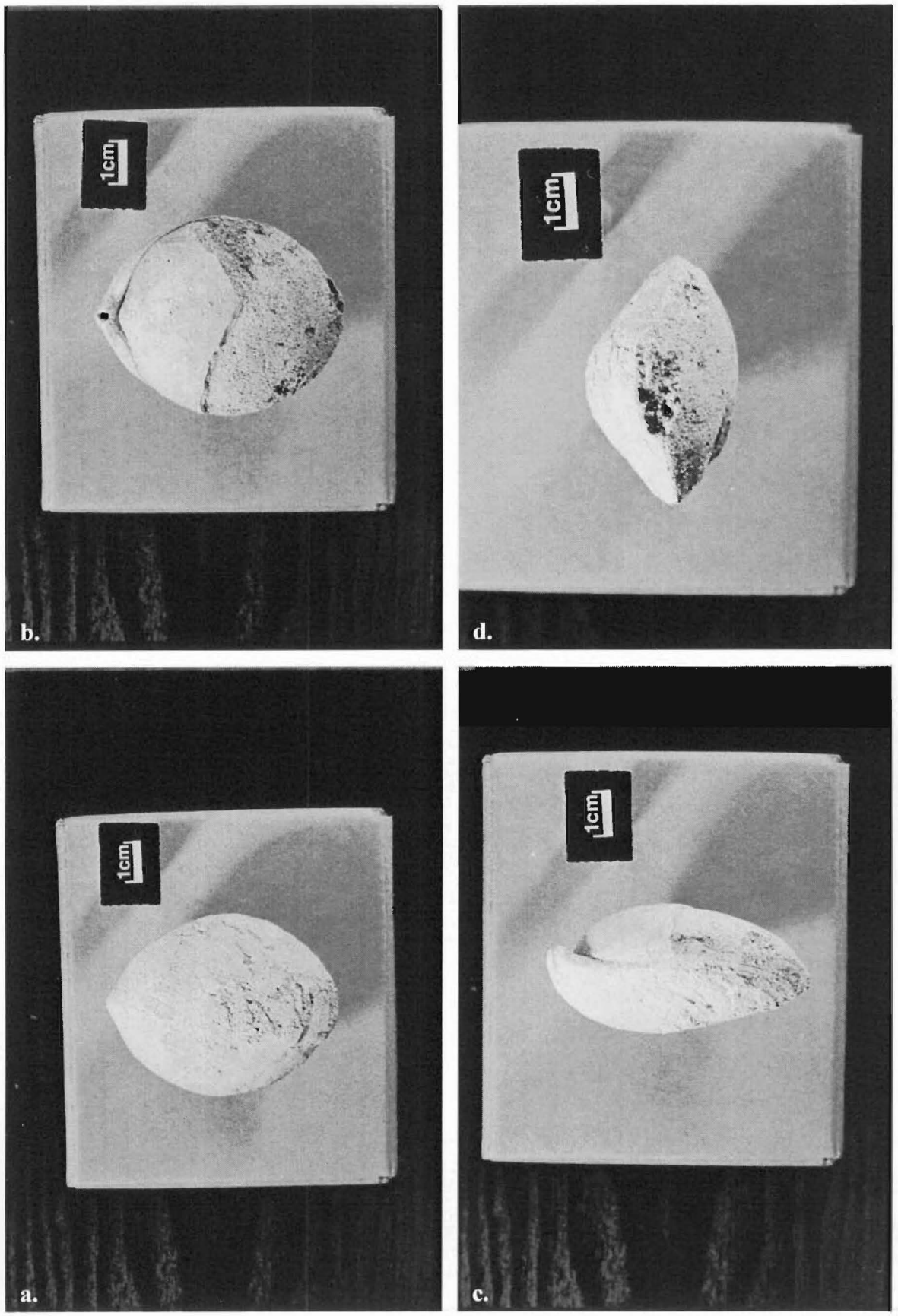


Figure 33. *Waitakia bartrumi* from Weka Pass (Allan Colln. 960).

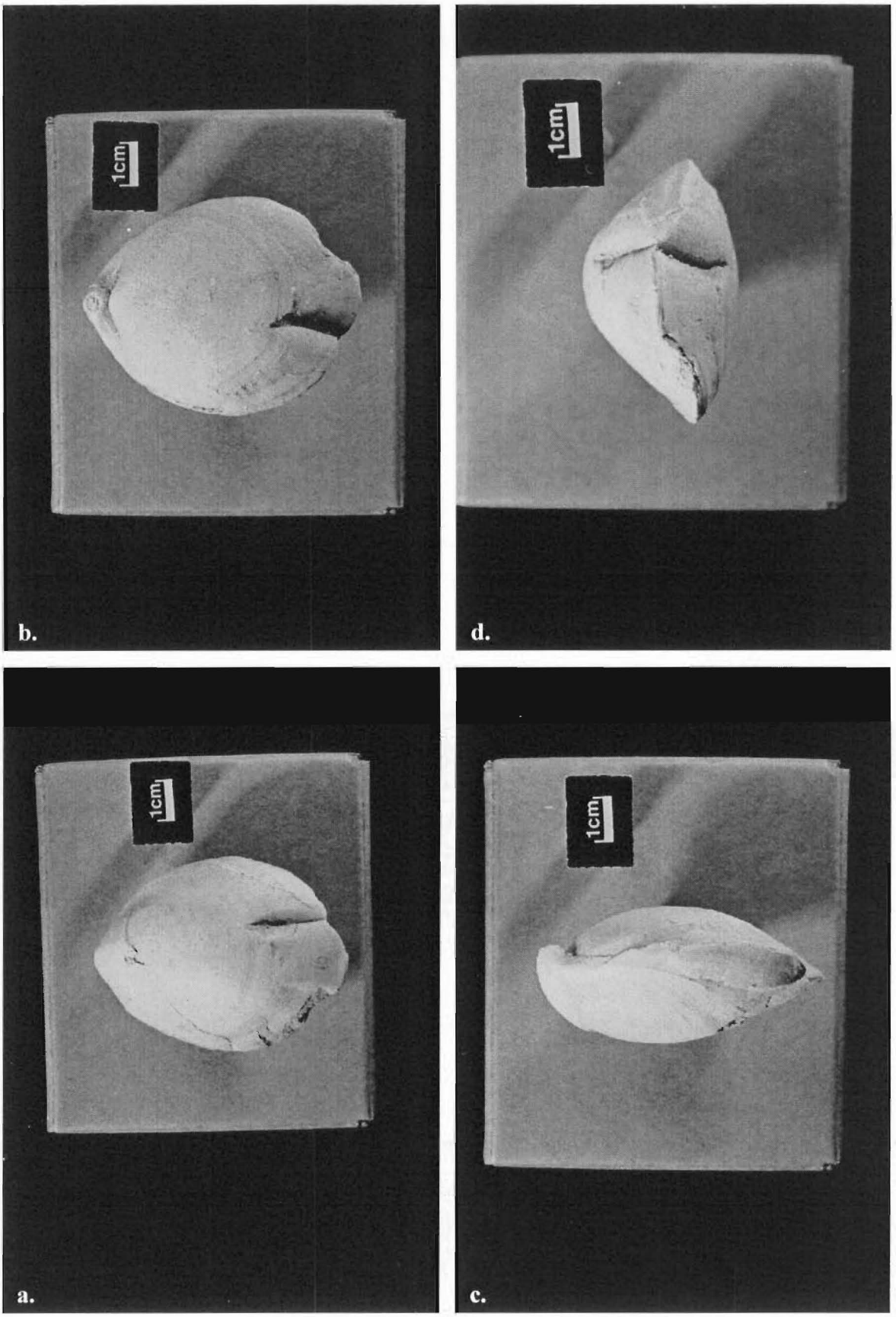


Figure 34. *Waitakia bartrumi* from Clifden (Allan Colln. 26270).

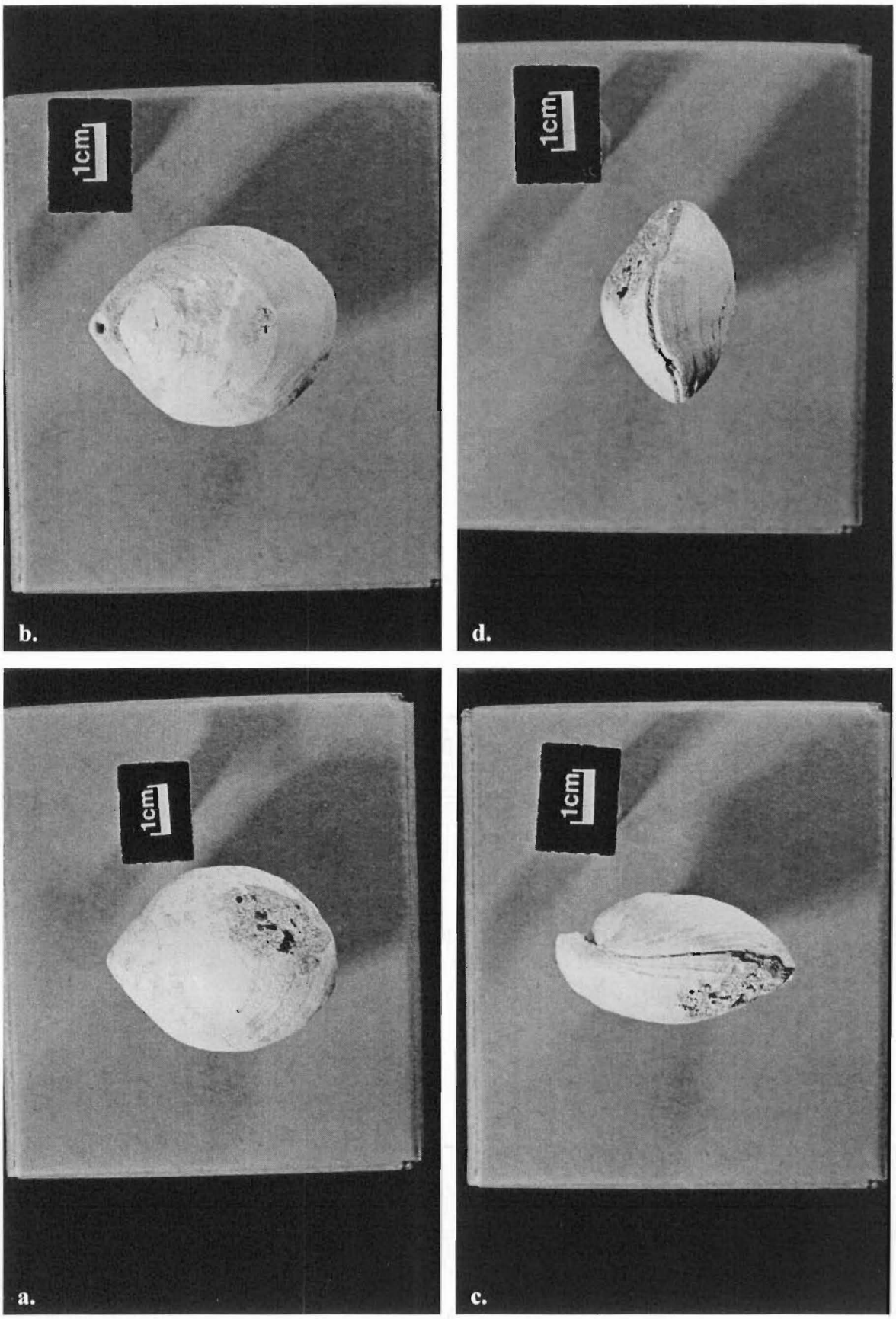


Figure 35. *Waitakia bartrumi* from Weka Pass (Allan Colln. 2338).

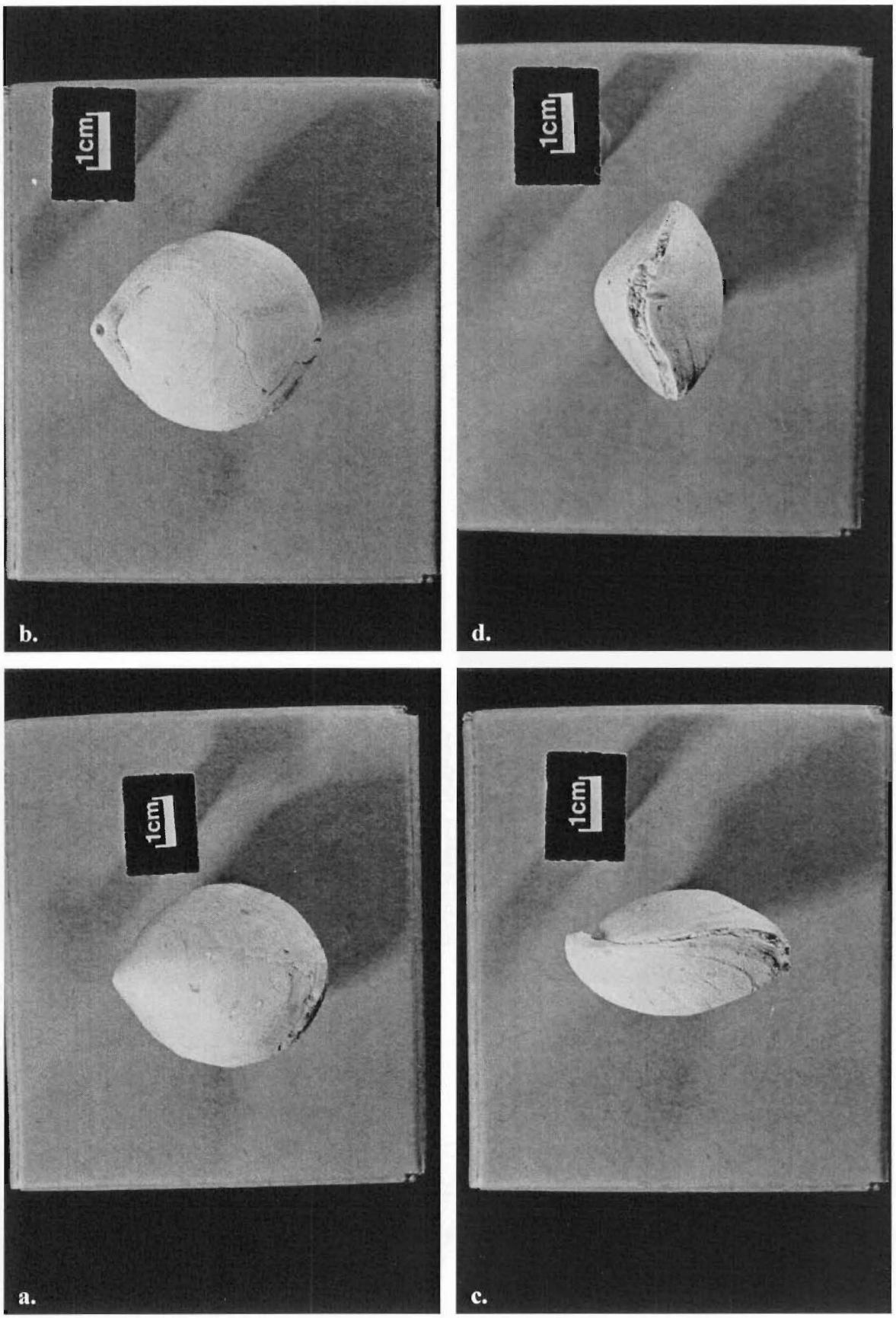


Figure 36. *Waitakia bartrumi* from Clifden (Allan Colln. 26310).

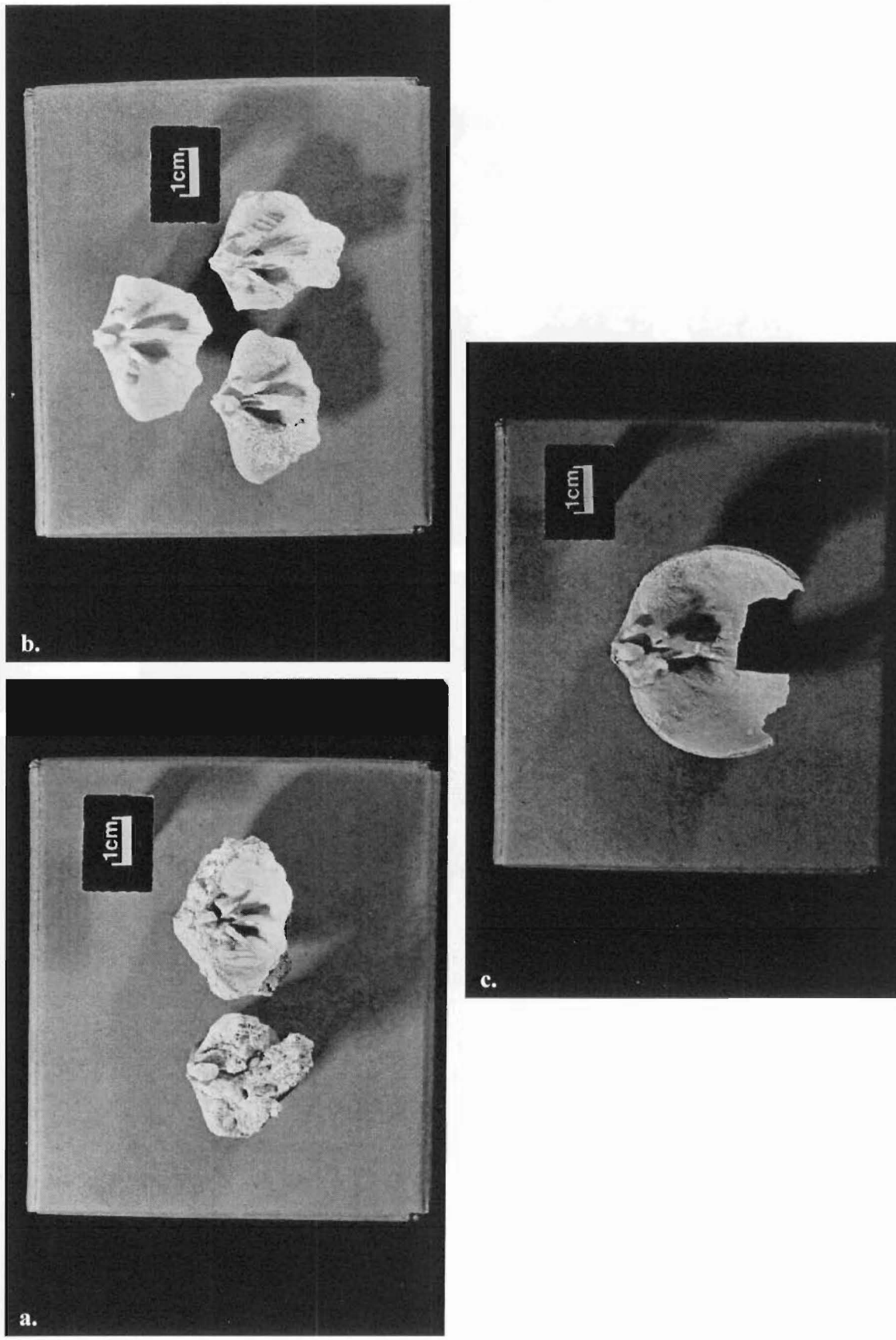


Figure 37. Dorsal interiors of *Waitakia bartrumi* from Weka Pass (**a**: UCM 2024, 2025), Clifden Quarry (**b**: UCM 2026, 2027, 2028), and Ward's Quarry (**c**: Allan Colln. 1328).

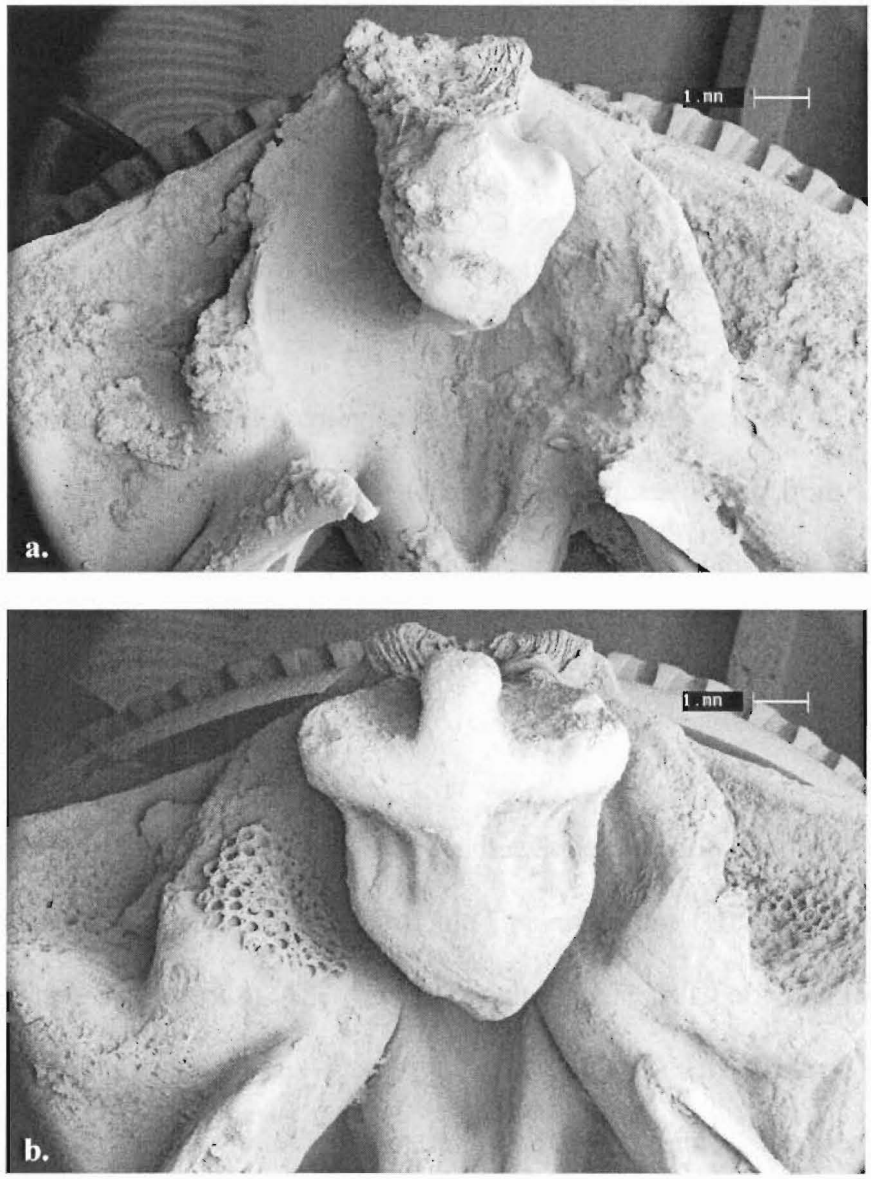


Figure 38. Dorsal interiors of *Waitakia bartrumi* from Weka Pass (**a**: UCM 2029) and Clifden Quarry (**b**: UCM 2030).

in strata of Lillburnian age (Lill Sand), indicates that *Waitakia* probably extends into Clifdenian strata before its necessary reference to *Neothyris* due to complete loss of the connecting band.

An interesting feature of the scatter-plot for Weka Pass and Clifden (graph 4) is the difference in length relative to width seen between the Weka Pass and Clifden material, as demonstrated by the change in slope of the regression line. This increase in length relative to width with geological age appears to be a general trend of the lineage, as when measured specimens of Otaian age *Waitakia haasti* from Deborah are added to the scatter-plot (graph 5), the regression line for the specimens demonstrates a still smaller width to length ratio than the Altonian Weka Pass specimens.

Waiparia bartrumi occurs abundantly in the Conglomeratic Member (Fleming et al. 1969; Lower Member of Allan 1937d) and Upper Member (Fleming et al. 1969; Middle and Upper Members of Allan 1937d) of the Forest Hill Formation in many Southland limestone quarries (i.e. Doherty's Quarry, Forest Hill Quarry, Ward's Quarry, etc.). It is found in the Conglomeratic and Upper Limestone Members at Clifden, and presumably at the aforementioned quarries, though the Member isn't always exposed. The basal Conglomeratic Limestone Member of the Forest Hill Formation is Otaian (c.f. Hyden 1979), the species in collections from Doherty's Quarry and Lady Barkly Quarry being *Waitakia cottoni*, the ancestor of *bartrumi*.

3.6 ***Waitakia cottoni*** (Thomson, 1920)

SYNONYMY: *Pachymagas cottoni* Thomson, 1920, p. 375-376, text fig. 8

Pachymagas cottoni Allan, 1937c, p. 132, 133, 134
Pachymagas forbesi Allan, 1937c (in part), p. 133, 134-135, pl. XVIII, figs. 1-2
Pachymagas haasti Allan, 1937c, p. 133, 135
Pachymagas hoodi Allan, 1937c, p. 133, 135, pl. XVIII, figs. 3-4
Pachymagas morgani Allan, 1937c, p. 133, 136
Pachymagas cottoni Allan, 1937d, p. 142, 145
Pachymagas hoodi Allan, 1937d, p. 142, 145
"*Pachymagas*" *cottoni* Allan, 1960, p. 246, 263 (stratigraphic range)
"*Pachymagas*" *forbesi* Allan, 1960 (in part), p. 246, 263 (stratigraphic range)
"*Pachymagas*" *haasti* Allan, 1960 (in part), p. 246, 264 (stratigraphic range)
"*Pachymagas*" *hoodi* Allan, 1960, p. 246, 264 (stratigraphic range)
"*Pachymagas*" *morgani* Allan, 1960 (in part), p. 246, 264 (stratigraphic range)
Pachymagas cottoni Levy, 1961, p. 83, 87
Pachymagas cottoni Keyes, 1971, p. 81-82
"*Pachymagas*" *cottoni* Dawson, 1990a, p. 63-64

TYPE LOCALITY: "Sands below main Mount Brown limestone (D), cuesta overlooking the Weka Pass" (Thomson 1920). The "Mount Donald horizon" (Allan 1937c and see fig. 11) at the base of the upper 'lens' (Browne & Field 1985) of the Main Mt Brown Limestone Member of the Mt Brown Formation, Weka Pass, North Canterbury.

TYPE MATERIAL: Holotype (Br 119) in the National Museum of New Zealand, Wellington. Holotype (UCM 1466a/Allan Colln. No. 1003) and two paratypes (UCM 1466b/Allan Colln. No. 1009) of *Pachymagas hoodi* in the Department of Geological Sciences, University of Canterbury, Christchurch.

(Source: Dawson 1990a)

OCCURRENCE: Main Mt Brown Limestone (base of) {North Canterbury}, at: Weka Pass; Sharks Tooth Hill Member, Forest Hill Formation {Southland}, at: Doherty's Quarry, Lady Barkly Quarry; Otaian greensands {South Canterbury}, at: Waihi River.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (1405-1440 Doherty's Quarry) ; (1541-1560 Doherty's Quarry) ; (26416-26428 Doherty's Quarry) ; (1000, 1002, 1005-1009, 1014, 1016, 1018, 1021, 1024-1027 Weka Pass) ; (26491-26524 Lady Barkly Quarry); (28495-28498 Weka Pass). Unnumbered collections, University of Canterbury: (Weka Pass (bag): D. I. MacKinnon Collection) ; (Weka Pass (bag): S. Fryer MSc. Thesis Collection). New Zealand Geological Survey: (Fossil Record Number J37/f9514, G.S. No. 3238, 18 conjoined valves and five dorsal interiors, Waihi River).

AGE/RANGE: Otaian-Altonian

FIGURES: 39-44

DECRIPTION: Large, smooth, biconvex shell displaying numerous faint growth-lines; shell suborbicular to broadly elliptical; wide cardinal margin almost straight, gently curved; anterior commissure weakly to moderately broadly unisulcate. Beak relatively compressed, obtuse, erect, attrite; large circular mesothyrid foramen; beak ridges well defined, bounding relatively prominent, wide ventral palintrope; gently convex cardinal area with conjunct deltidial plates ranging to low, wide symphytium. Median septum thick, extending anteriorly one-third or less of valve length, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped hinge-trough with steeply inclined walls; the hinge-plates, fused medially with the septum, often

becoming detached from the septum anteriorly; crural bases fused to the thickened inner socket ridges. Cardinal process consisting of roughened myophore with large bulbous anterior swelling that projects ventrally occupies two-thirds of the hinge-trough; wing-like projections of myophore develop posteriorly; a prominent median ridge is sometimes displayed along the upper part of the process, either side of which the diductor muscles ran to attach posteriorly. Dorsal adductor muscle scars are large and distinct, terminating anteriorly just beyond the termination point of the short median septum – at one-third the length of the valve. The teeth are large and sturdy, and are perched on swollen bases, which are grooved to accommodate the swollen inner socket ridges. Adult loop trabecular.

DISCUSSION: Allan's (1937c) species *Pachymagas hoodi* from the Mount Donald horizon he regarded as "related to *P. cottoni* Thomson from the same horizon but differs in being more ovate, has more convex sides and a more curved hinge-line" (Allan 1937c, p. 135). In this study it is interpreted that Allan's above observed differences between *hoodi* and *cottoni* can better be explained as differences due to phenotypic variation rather than to separate specific identity. Also interpreted in this manner are Allan's (1937c) record of *Pachymagas forbesi*, *P. haasti*, and *P. morgani* from the same horizon. The differences in exterior shell shape that led Allan to discriminate these three species from the Mount Donald horizon are, again, interpreted to be a reflection of phenotypic variation rather than specific difference.

Waitakia cottoni is, simply put, a more evolved representative of *W. marshalli*, itself found in strata of Waitakian and Otaian ages. The Otaian representative of *W. cottoni* from Waihi River resembles *W. marshalli* very closely exteriorly, being almost ventribiconvex, as are some occurrences of *W. marshalli*. Interiorly, however,

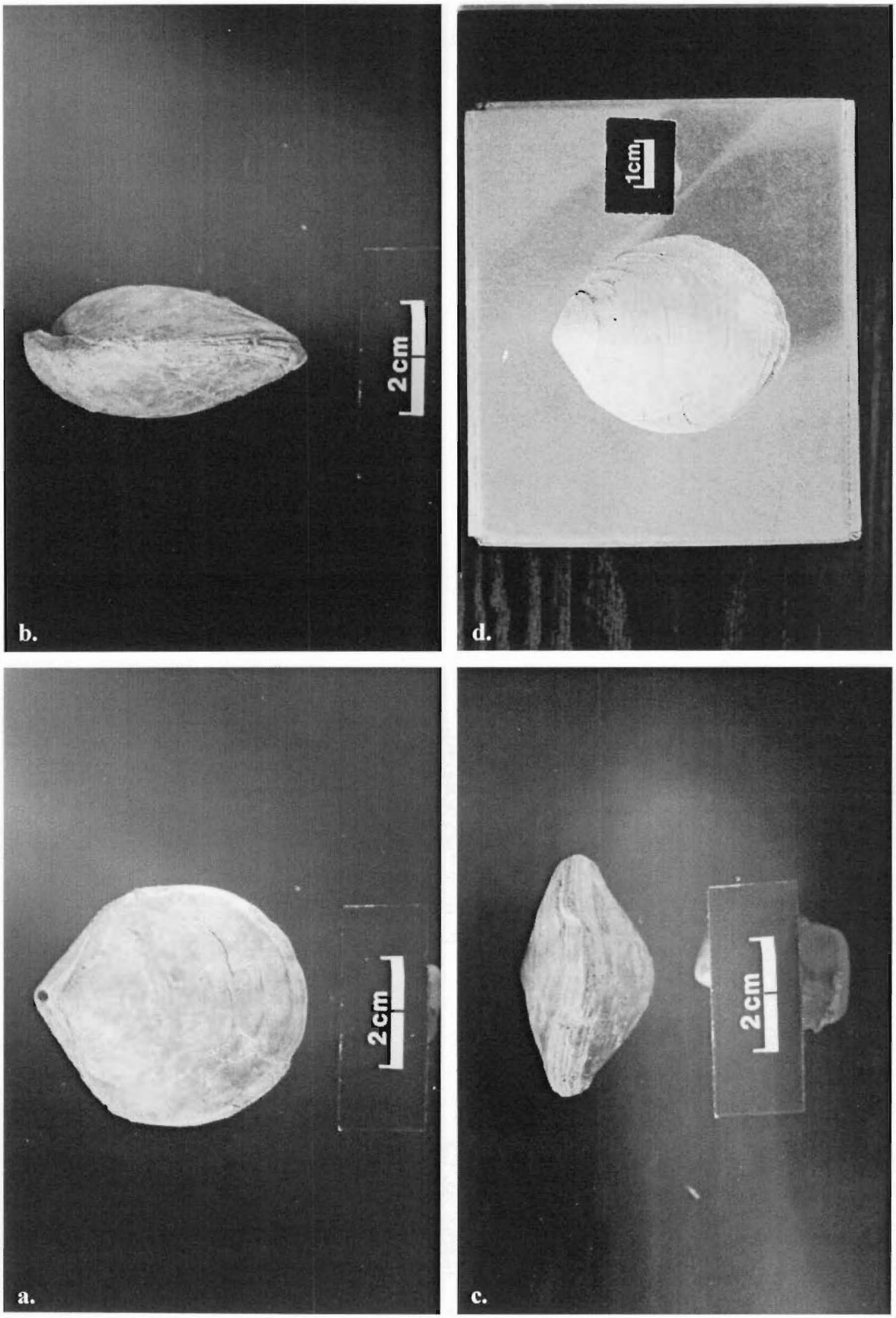


Figure 39. Holotypes of *Pachymagas cottoni* (**a**, **b**, **c**: Br 119) and *P. hoodi* (**d**: Allan Colln. 1003).

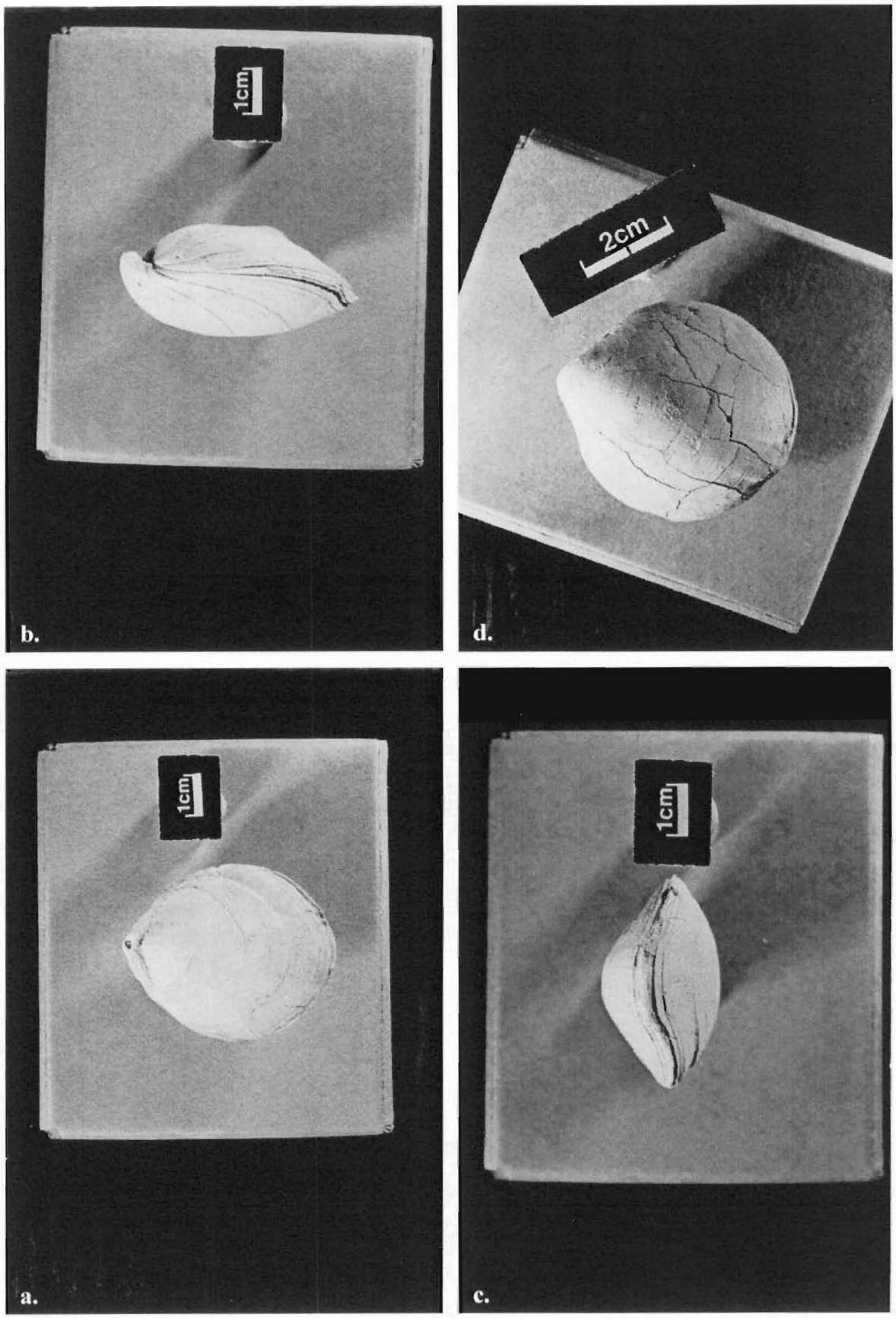


Figure 40. Holotype of *Pachymagas hoodi* (**a**, **b**, **c**: Allan Colln. 1003) and ventral valve of *Waitakia cottoni* (**d**: GS 3238; from Waihi River).

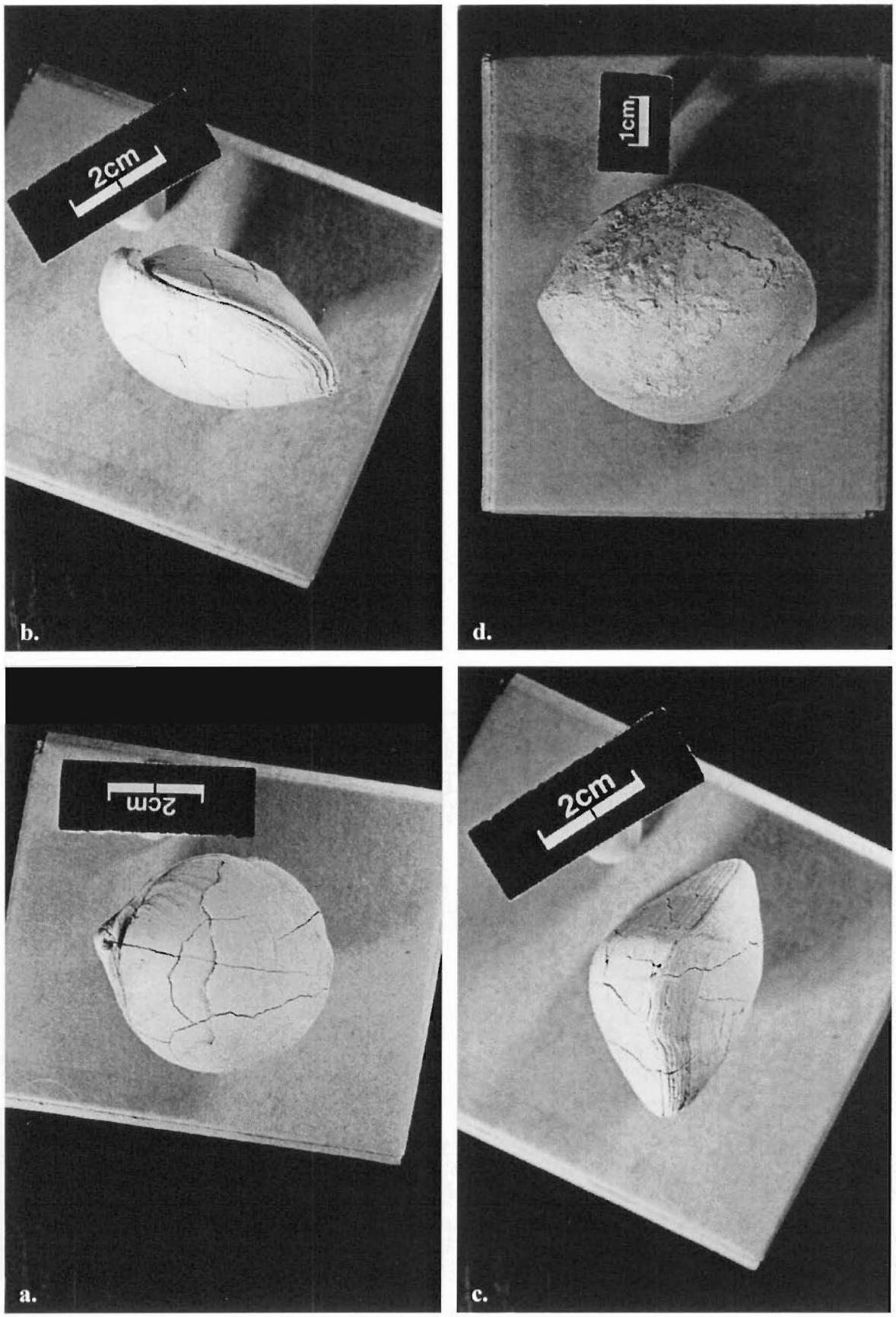


Figure 41. *Waitakia cottoni* (**a**, **b**, **c**: GS 3238; Waihi River; **d**: Allan Colln. 1005; Weka Pass).

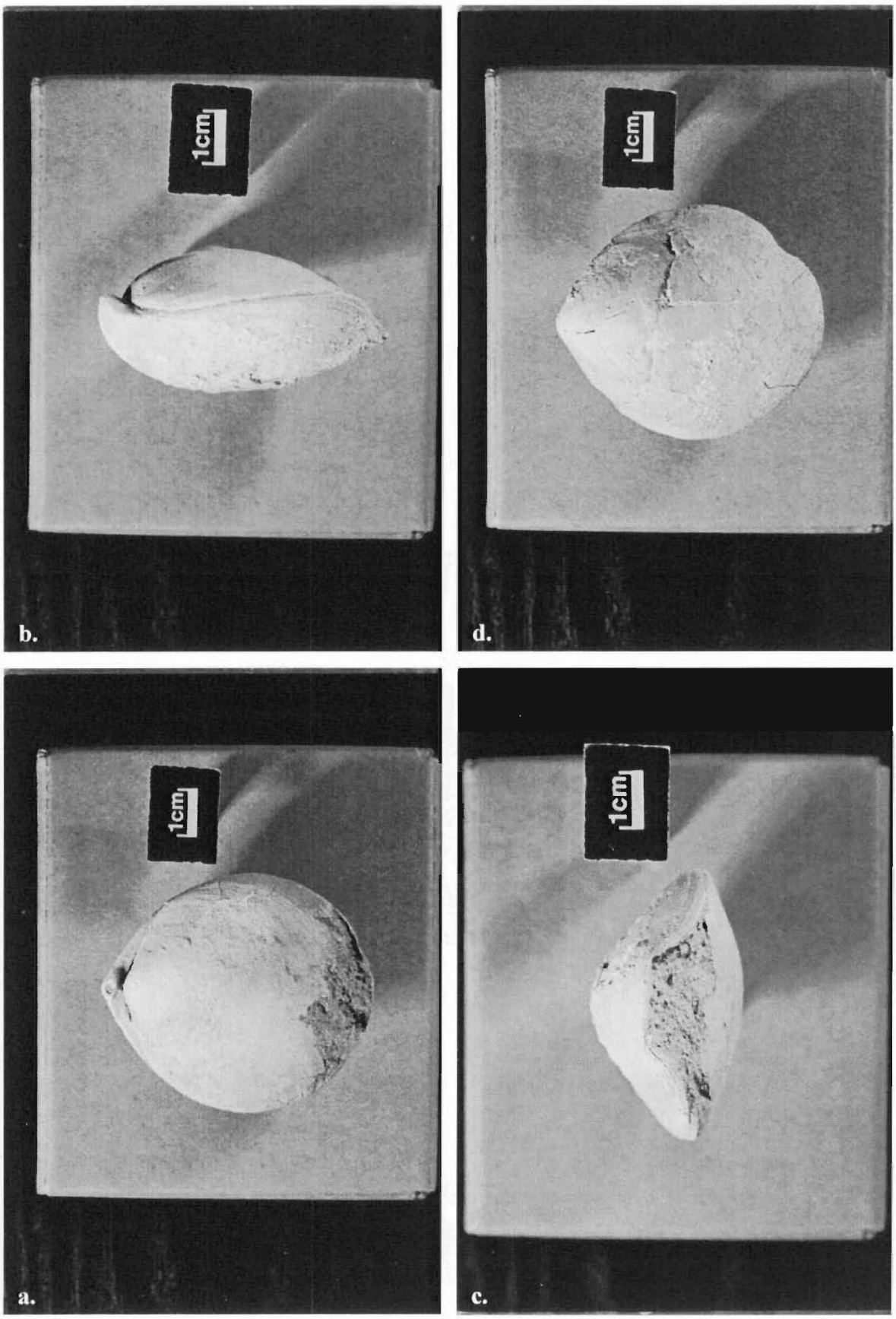


Figure 42. *Waitakia cottoni* (**a**, **b**, **c**: Allan Colln. 1005; **d**: UCM 2010) from Weka Pass.

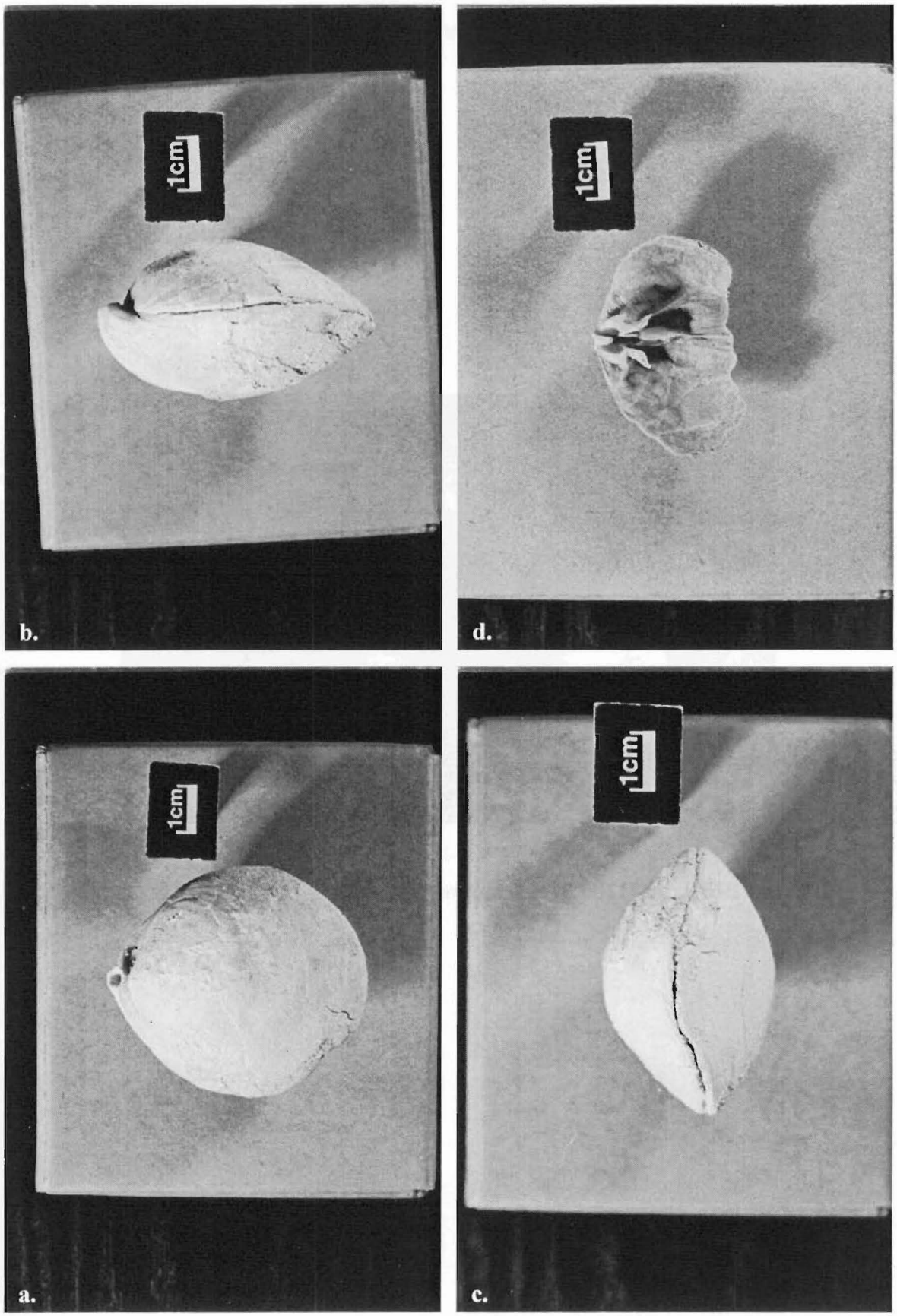


Figure 43. *Waitakia cottoni* (**a**, **b**, **c**: UCM 2010; Weka Pass; **d**: GS 3238; Waihi River).

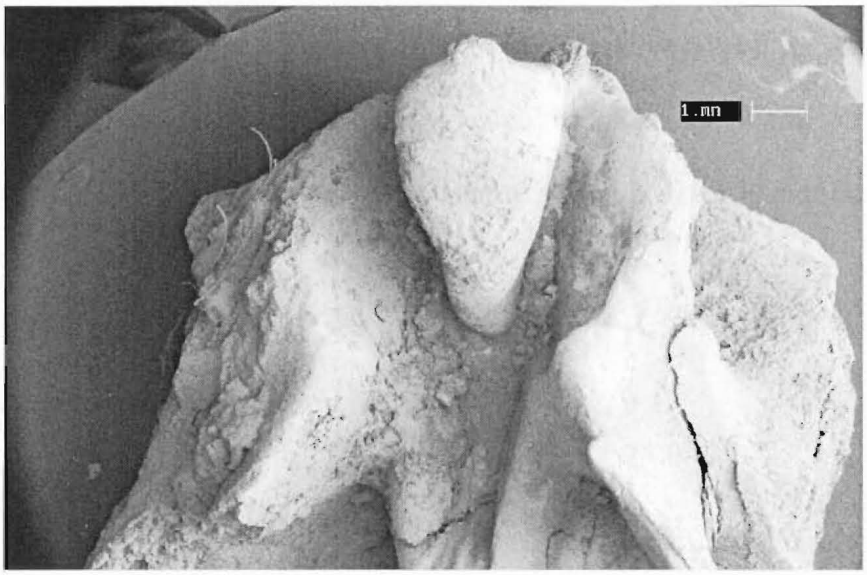


Figure 44. Dorsal interior of *Waitakia cottoni* (UCM 2011) from Weka Pass.

the Waihi River species is differentiated from *W. marshalli* by possession of a steep-walled hinge-trough, a large well-developed cardinal process, a very short median septum and hinge-plates that are partially detached from the septum anteriorly (Fig. 43d). The specimens from Waihi River are found in a very highly glauconitic calcareous very fine sand, and are notable in that the beaks are more compressed than in the forms found at Weka Pass and at Lady Barkly and Doherty's quarries, the septum too being somewhat shorter than at these localities. The posterior thickening and short septum observed in *W. cottoni* is interpreted to have helped weight the shell posteriorly; evidently the environment in which the form at Waihi River lived required the shell to be highly convex and posteriorly weighted for life on the unstable substrate.

3.7 ***Waitakia elliptica*** (Thomson, 1918)

SYNONYMY:

Magellania insolita Hutton, 1905 (in part), p. 476, not pl. XLV, fig. 5 (not the species of Tate, 1880)
Pachymagas ellipticus Thomson, 1918a, p.118
Pachymagas (?) *ellipticus* (referred to *Waiparia*) Thomson, 1927, p. 285
Waiparia (?) *elliptica* Allan, 1937a, p. 125-126, pl. XVI, fig. 6
Waiparia (?) *elliptica* Allan, 1957, p. 106
Waiparia (?) *elliptica* Allan, 1960, p. 239
Waiparia (?) *elliptica* Keyes, 1971, p. 83
Waiparia (?) *elliptica* Dawson, 1990a, p. 76-77
Waiparia elliptica MacKinnon, Beus & Lee, 1993, p. 346, fig. 12 [10-23]

TYPE LOCALITY: "Greensands below the Maerewhenua limestone, Waitaki Valley" (Uttley). "The type was almost certainly collected in the neighbourhood of Duntroon." (Allan 1957, p. 106)

TYPE MATERIAL: Holotype (Br 1268) and paratypes (Br 1269 ; B 443) in the National Museum of New Zealand, Wellington. Paratypes (B46, Hutton's *Magellania insolita* Tate from Duntroon, and labelled paratype of *P. elliptica* by Thomson ; B47, figured by Allan (1937a)) in Canterbury Museum, Christchurch.

(Source: Dawson 1990a)

OCCURRENCE: Kokoamu Greensand {North Otago}, at: Landon Creek, Kokoamu Bluff, Duntroon, Earthquakes, {South Canterbury}, at: Haugh's Quarry, Squires Farm, Smite River, McCulloughs Bridge; Otekaike Limestone {South Canterbury}, at: Waihao Basin; Stavely limestone and greensand {South Canterbury}, at: Stavely Quarry; Weka Pass Stone {North Canterbury}, at: Mt. Grey, Onepunga; greensand {Westland}, at: Karetu River, Grey River.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (1-165 Waihao) ; (456-489 Otaio Gorge) ; (588-650 Maerewhenua River) ; (1033-1185 Duntroon) ; (1561-1563 Earthquakes) ; (1565-1615 Earthquakes) ; (1617 – 1632 Earthquakes) ; (7000-7115 Duntroon) ; (7116-7295 Duntroon) ; (7296-7418 Duntroon) ; (27018 Earthquakes) ; (27427 Kokoamu Bluff) ; (28763 Grey River). Unnumbered collections, University of Canterbury, Department of Geological Sciences: (Haugh's Quarry (bag): D. I. MacKinnon Collection) ; (Squires Farm (box): collected by S. Beus). Unnumbered collections, National Museum of New Zealand, Wellington: (Stavely Quarry (bag): collected by R. Speight) ; (Stavely Quarry (bag): collected by J. A. Thomson).

AGE/RANGE: Duntroonian

FIGURES: 47-49

DESCRIPTION: Small to medium-sized, smooth, biconvex shell; broadly ovate or subrounded in outline; cardinal margin moderately curved; anterior commissure rectimarginate to incipiently unisulcate. Beak obtuse, erect; small circular foramen variable in type – mesothyrid or submesothyrid, but does range to hypothyrid; beak ridges fairly well defined; gently convex cardinal area with conjunct deltidial plates. Median septum slender, extending anteriorly one-third to one-half of valve length, bifurcating posteriorly to unite with the relatively steeply inclined hinge-plates, forming an excavate hinge-trough (septalium) in juveniles which is infilled during growth and is not found in adults; crural bases fused to the thickened inner socket ridges. Cardinal process consisting of roughened myophore is small and pyramidal, confined to the posterior portion of the hinge-trough, developing a boss-like anterior swelling with growth; the cardinal process occupies the posterior one-third of the hinge-trough, often tapering anteriorly to occupy up to one-half of the hinge-trough; incipient wing-like projections of myophore develop posteriorly. Dorsal adductor muscle scars relatively large and distinct, terminating anteriorly at approximately the termination point of the median septum – at one-third to one-half the length of the valve. The relatively large muscle-field scars of the ventral valve are impressed such as to produce a low median ridge in the valve floor between the scars. The teeth are large and sturdy, and are perched on swollen bases, which are grooved to accommodate the swollen inner socket ridges. Adult loop trabecular, the transverse connecting band attenuated.

DISCUSSION: *Waitakia elliptica* is a Duntroonian form, the earliest species attributed to *Waitakia*. Thomson (1920) initially considered that the species had arisen

as an offshoot of *Waiparia*, developing from *Waiparia abnormis*. This was due to possession of a submesothyrid foramen – having, like *W. abnormis*, lagged behind all other species of "*Pachymagas*" in foraminal evolution, but possessing a more evolved foramen than *W. abnormis'* hypothyrid type. Thomson (1927, p. 285) noted that *Pachymagas ellipticus* (*W. elliptica*) has an earlier occurrence than does *W. abnormis* – a Duntroonian or older common ancestor could be implied, though it is considered (section 4.0) that *W. abnormis* could be a descendent of *Waitakia elliptica*.

A notable feature of *Waitakia elliptica* is the variability of the foramen – the type of foramen (following Thomson's 1927 (p. 71-72, fig. 20) terminology) seems in the majority of specimens to be mesothyrid, but almost an equal number of specimens possess submesothyrid foramina; the hypothyrid type does occur, but is not common. Phylogenetic implications of the variability in foramen type displayed by *W. elliptica* are discussed in section 4.0.

Graph 6 displays a histogram of length for *Waitakia elliptica*, while graph 7 demonstrates the allometric hypermorphosis (see McKinney and McNamara 1991, and fig. 45 and table 7) occurring in the lineage. Note that *Waitakia haasti* is not considered an immediate descendent of *W. elliptica* (Duntroonian), but rather descends first through *W. marshalli* (Waitakian), and then, possibly, through *W. alldayi* (Otaian). Graph 8 demonstrates, on a pedicle valve vs. width plot, the interpreted sequence of descent. Graph 8 does not tell the whole story, as descent from *W. marshalli* is first through *W. alldayi* and then to *W. haasti*; *Waitakia alldayi* is not shown on the plot for reasons of clarity. See section 4.0 for further discussion on the phylogeny of *Waitakia* and *Waiparia*.

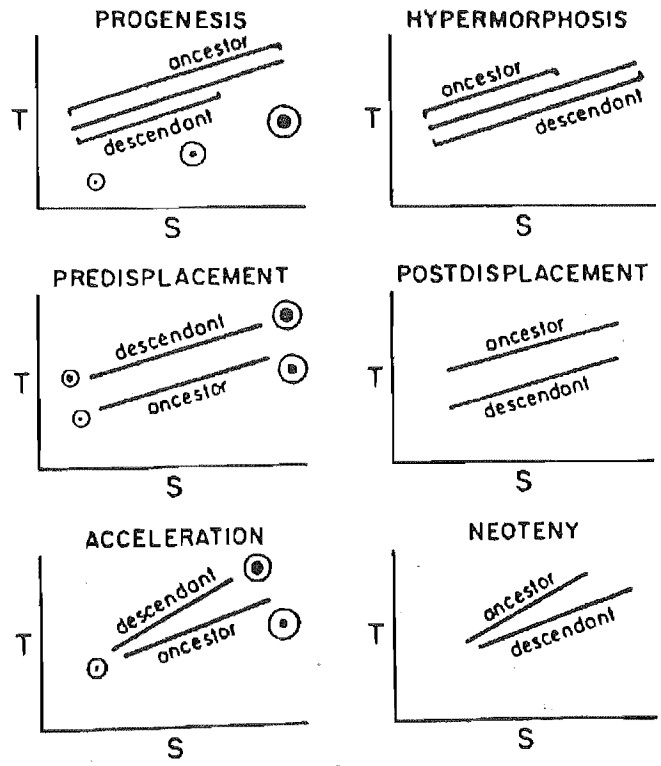
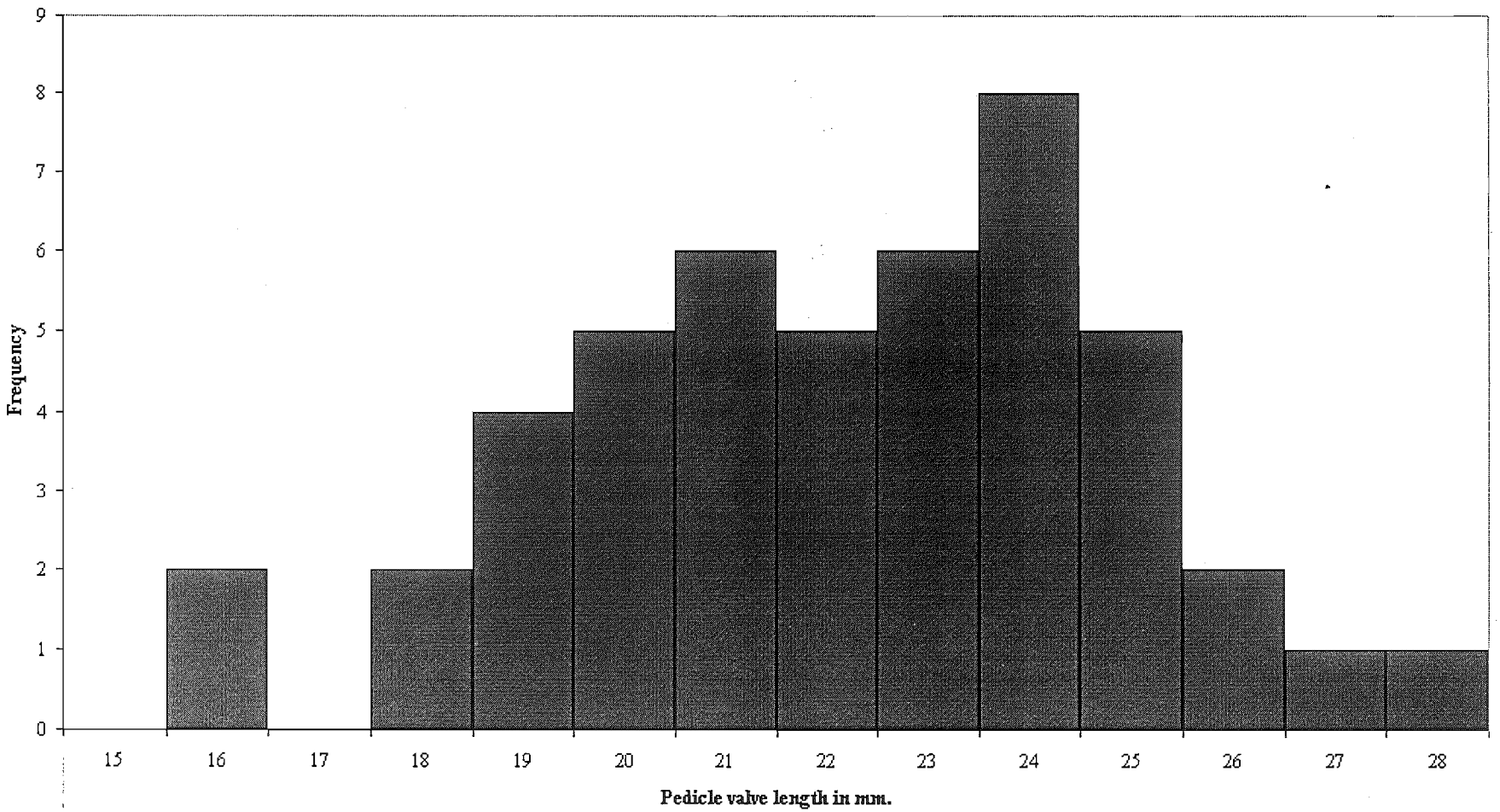


Figure 45. "Allometric" heterochrony, demonstrated by ontogenetic graphs for related species. S = Body Size (length, weight etc.) while T = trait measurement; both S and T can be log-transformed or untransformed. The open circle illustrates body size while the closed circle is a 'trait', such as organ size etc. (From McKinney & McNamara 1991)

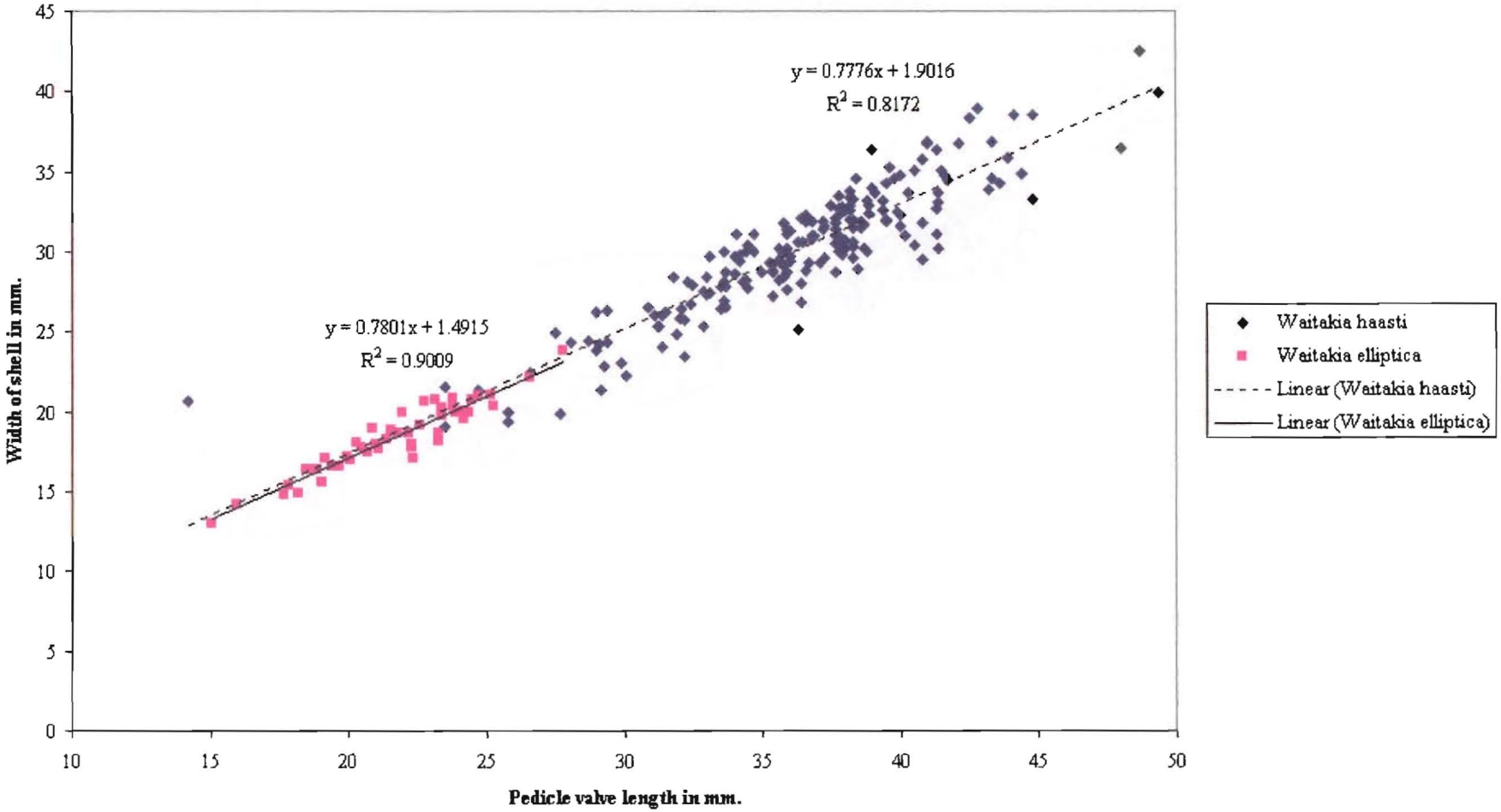
	Trajectory of descendant species relative to ancestor		
Allometric term	Slope (or curve shape)	*y*-intercept	Adult body size
Allometric progenesis (= ontogenetic scaling)	Same	Same	Smaller
Allometric hypermorphosis (= ontogenetic scaling)	Same	Same	Larger
Allometric neoteny (= shape dissociation)	Lower	Same	May vary
Allometric acceleration (= shape dissociation)	Higher	Same	May vary
Allometric predisplacement (= shape dissociation)	Same	Greater	May vary
Allometric postdisplacement (= shape dissociation)	Same	Less	May vary

Table 7. Table illustrating the terms of "Allometric" heterochrony which are defined by comparison of the ontogenetic trajectories of descendent species relative to ancestral species, as shown in Figure 45 above. The synonyms demonstrated in parentheses are from Shea (1988). (From McKinney & McNamara 1991)

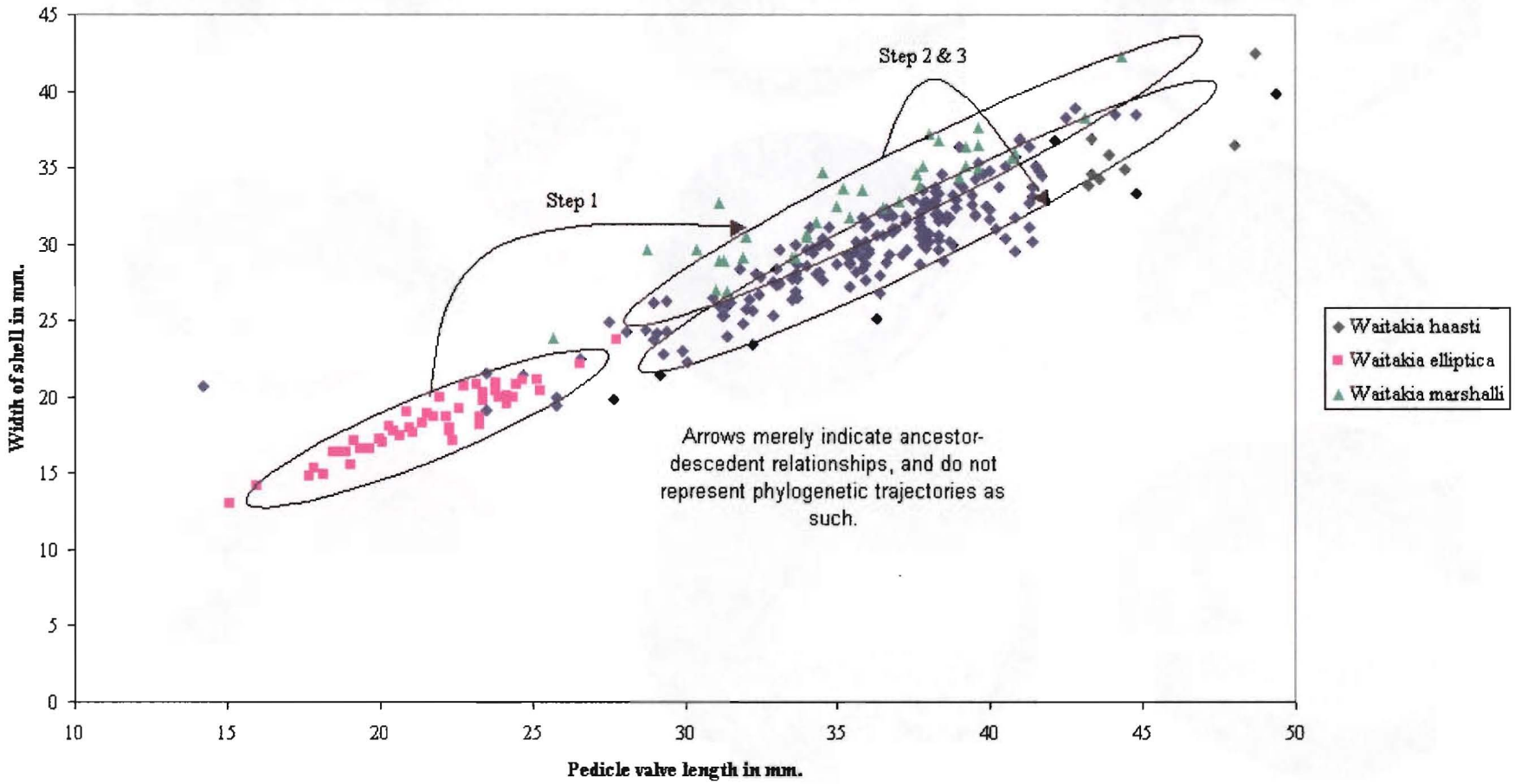
Graph 6: Histogram of pedicle valve length for Waitakia elliptica from Kokoamu Bluff



Graph 7: Pedicle valve length vs. Width for Waitakia haasti and Waitakia elliptica



Graph 8: Pedicle valve length vs. Width for Waitakia haasti, Waitakia elliptica, and Waitakia marshalli, and showing interpreted sequence of descent (W. alldayi (step 3) is left out for reasons of clarity)



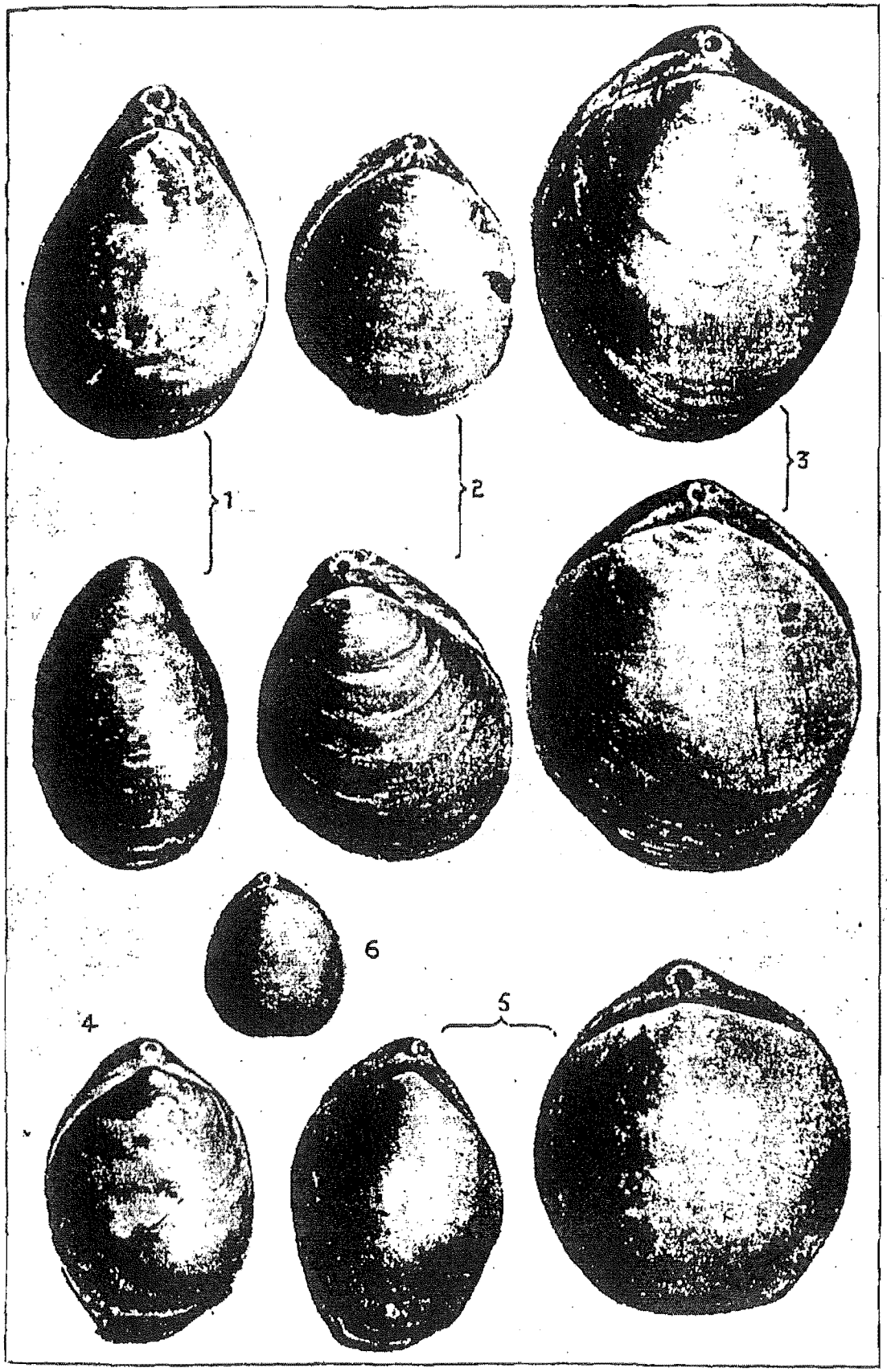


Figure 46. Hutton's (1905) description of *Magellania insolita* appears to be partly based on material now referred to *Waitakia elliptica* and *W. marshalli*. Specimen 5 (right) above appears to be *Waitakia marshalli* of this study. Enlarged. (From Hutton 1905)

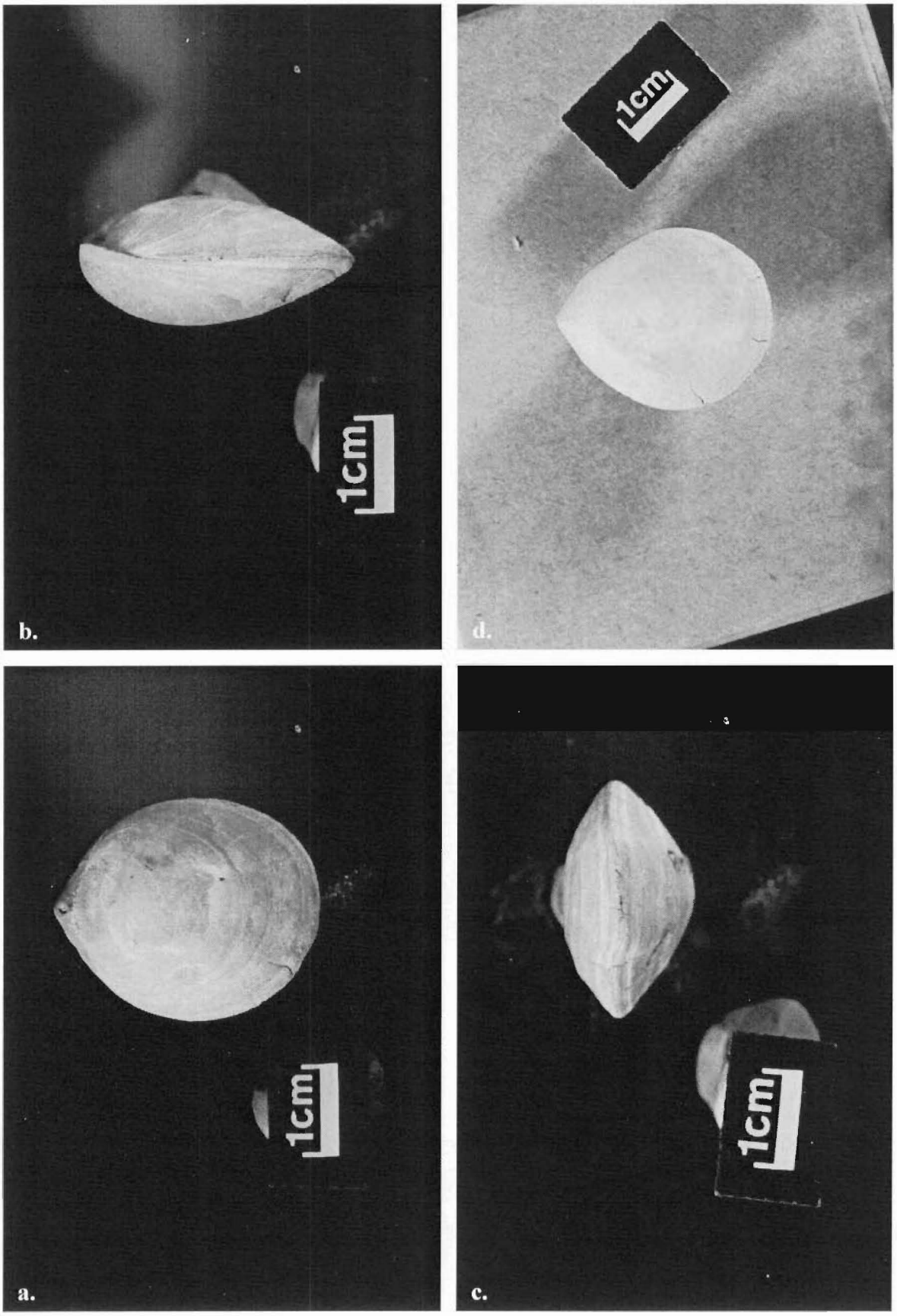


Figure 47. Holotype of *Waiparia elliptica* (**a**, **b**, **c**: Br 1268) and ventral exterior of *Waitakia elliptica* (**d**: Allan Collection 1046; from Duntroon).

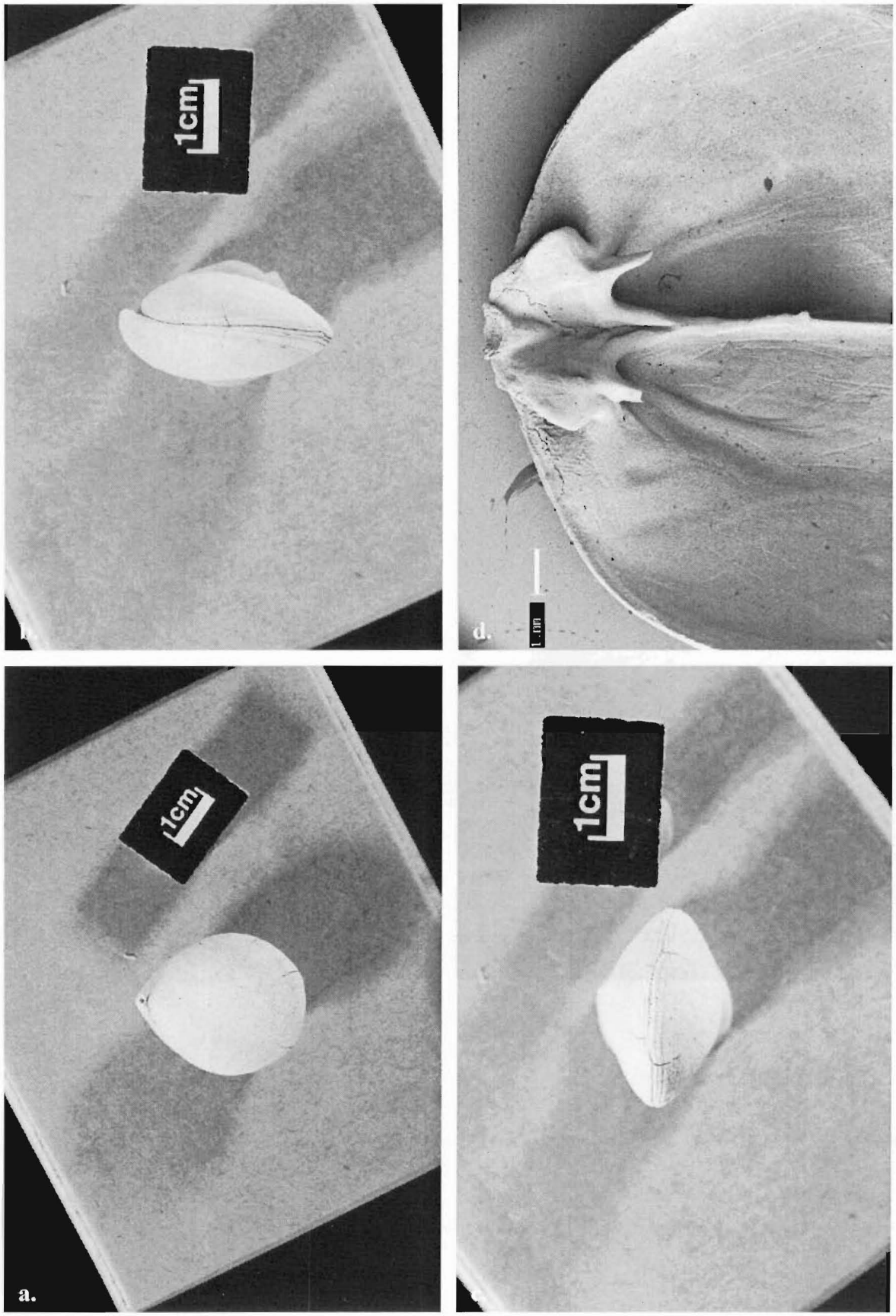


Figure 48. Exteriors (**a**, **b**, **c**: Allan Colln. 1046; Duntroon) and dorsal interior (**d**: UCM 2014; Haugh's Quarry) of *Waitakia elliptica*.

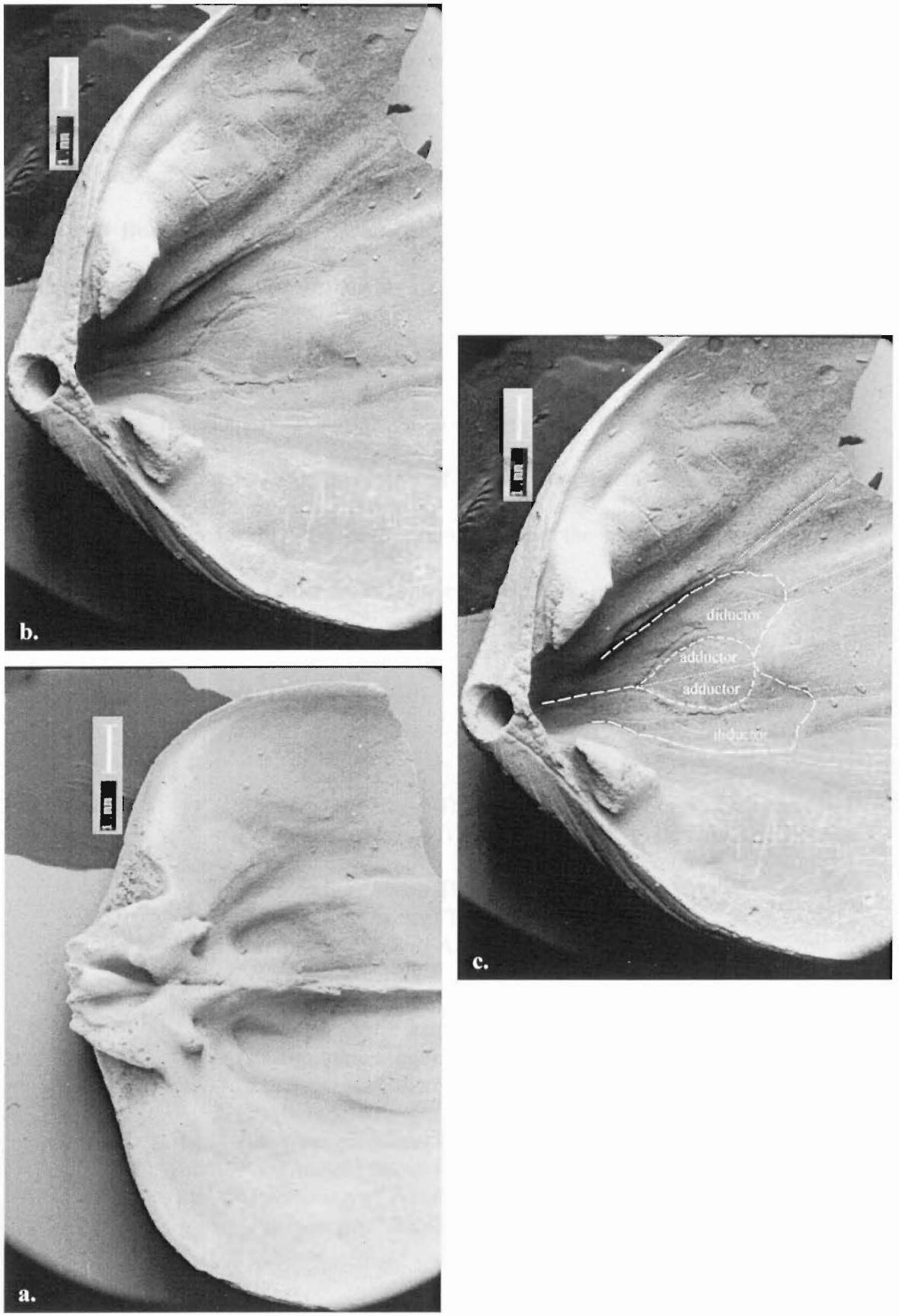


Figure 49. Dorsal (**a**: UCM 2015) and ventral (**b**, **c**: UCM 2016) interiors of *Waitakia elliptica* from Haugh's Quarry. **c.** demonstrates muscle scars (labelled) and mantle canals (linear features).

The description of *Magellania insolita* Hutton 1905 (here synonymised) appears to have been partly based on *W. elliptica* from Duntroon; additional description seems to have been derived from Curiosity Shop material – *Waitakia marshalli* from the Berrydale Greensand exposed at that locality. Hutton's figure (reproduced here as figure 46) seems to demonstrate a specimen of *W. marshalli*, doubtless from Curiosity Shop.

From fragmentary material Allan (1940, p. 295) recorded the possible occurrence of *W. elliptica* in limestone of the Chatton Formation, Balfour Quarry. Material from this locality has been examined, and the conclusion drawn that *W. elliptica* does not occur , rather the descendent species *W. marshalli* is present.

3.8 ***Waitakia haasti*** (Thomson, 1920)

SYNONYMY:

Pachymagas haasti Thomson, 1920, p. 377, pl. XXV, figs. 4-7
Pachymagas hectori Thomson, 1920, p. 377, pl. XXIV, figs. 10-13
Pachymagas haasti Thomson, 1926, p. 150
Pachymagas hectori Thomson 1926, p. 150
Pachymagas haasti Allan, 1937c, p. 135
"*Pachymagas*" *haasti* Allan, 1957, p. 106
"*Pachymagas*" *hectori* Allan, 1957, p. 106
"*Pachymagas*" *hectori* Allan, 1960, p. 241, 244, 264 (stratigraphic range)
"*Pachymagas*" *haasti* Allan, 1960, p. 241, 244, 246, 264 (stratigraphic range)
Pachymagas haasti Keyes, 1971, p. 82
Pachymagas hectori Keyes 1971, p. 82
"*Pachymagas*" *haasti* Dawson, 1990a, p. 65
"*Pachymagas*" *hectori* Dawson, 1990a, p. 66

TYPE LOCALITY: Gee Greensand, Deborah, North Otago.

TYPE MATERIAL: Holotype (Br 124) and paratype (Br 1338) in the National Museum of New Zealand, Wellington. Holotype (Br 1339) of *Pachymagas hectori* in the National Museum of New Zealand; paratype (B4) in Canterbury Museum, Christchurch.

(Source: Dawson 1990a)

OCCURRENCE: Gee Greensand {North Otago}, at: Deborah, Landon Creek, Rifle Butts, Devil's Bridge.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (1456-1464 Deborah railway cutting) ; (1466-1476 Deborah railway cutting) ; (26818-26881 Deborah) ; (26882-26948 Deborah) ; (26952-27014 Deborah) ; (27802-27853 Rifle Butts) ; (27857-27861 Rifle Butts) ; (1928-1999 Devil's Bridge) ; (2020-2072 Devil's Bridge) ; (27528-27531, 27534-27542, 27544-27603 Landon Creek). Unnumbered collections, University of Canterbury: (Rifle Butts (3 bags), Deborah road cutting (bag), Deborah railway cutting (bag), Landon Creek (2 bags): S. Fryer MSc. Thesis Collection) ; (Landon Creek (2 bags), Devil' Bridge (2 trays): D. I. MacKinnon Collection).

AGE/RANGE: Otaian

FIGURES: 50-53

DESCRIPTION: Medium to large, smooth, biconvex shell displaying numerous faint growth-lines; shell ovate; moderately wide cardinal margin gently curved; anterior

commissure moderately broadly unisulcate. Beak fairly low, obtuse, erect, attrite; moderately large mesothyrid foramen; beak ridges fairly well defined; gently convex cardinal area with conjunct deltidial plates. Median septum relatively thickened, extending anteriorly about one-third of valve length, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped hinge-trough with steeply inclined walls; crural bases fused to the thickened inner socket ridges; swelling-together of the crural bases confines the dorsal pedicle adjustor muscle attachment sites to the posterior of the hinge-trough. Cardinal process consisting of roughened myophore is small and pyramidal in juveniles, confined to the posterior portion of the hinge-trough; with growth the cardinal process develops a boss-like anterior swelling that projects ventrally; the adult cardinal process occupies the posterior one-third of the hinge-trough, often tapering anteriorly to occupy up to one-half of the hinge-trough; wing-like projections of myophore develop posteriorly; process displays incipient development of a median ridge along its upper part – the diductor muscles ran either side of this ridge to attach posteriorly. Dorsal adductor muscle scars are large and distinct, terminating anteriorly at approximately the termination point of the median septum – at one third the length of the valve. The large muscle-field scars of the ventral valve are impressed such as to produce a low median ridge in the valve floor between the scars. The teeth are large and sturdy, and are perched on swollen bases, which are grooved to accommodate the swollen inner socket ridges. Adult loop trabecular, the transverse connecting band very attenuated.

DISCUSSION: Brachiopods of the *haasti-hectori* (*P. hectori* is a junior synonym – see synonymy above) assemblage occur in great numbers in the base of the Otaian greensands at Landon Creek, Deborah, Devil's Bridge, and Rifle Butts. These have

been described as "...polymorphic swarms of large brachiopods placed by Thomson in the South American genus *Pachymagas*." (Allan 1960, p. 241) .

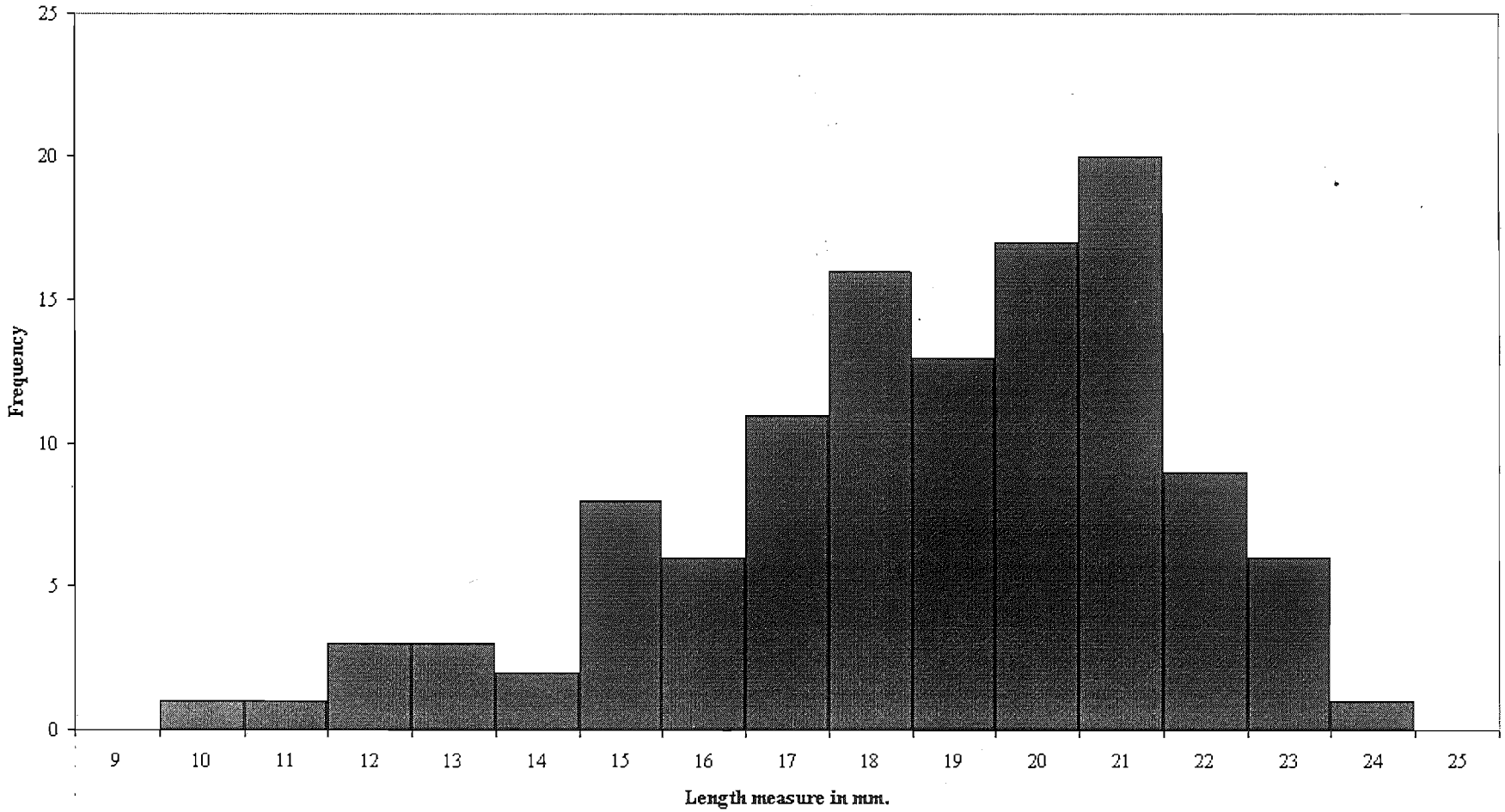
In Thomson's original descriptions, *hectori* differs from *haasti* only in its possession of an ovate outline (Thomson 1920, p. 377). An attempt was made to test the validity of this statement statistically; appropriate measurements were taken and graphed in aid of assessing any shape differences. It was considered that graphed data for a measure of shell length at maximum measured shell width was most likely to demonstrate the purported shape difference. Graph 9 displays a histogram constructed from data measured from material at Devil's Bridge, a locality at which Thomson (1926) stated both haasti and hectori occur. The histogram of graph 9 has one mode, where two modes might be expected if Thomson's stipulated shape difference existed. Graphs 10, 11, 12 and 13 demonstrate histograms constructed for pedicle valve length of material from Deborah (graph 10) and Devil's Bridge (graph 11), and of shell width for material from Deborah (graph 12) and Devil's Bridge (graph 13). All of these graphs demonstrate one prominent mode. Of note is the fact that the modes differ slightly between the two localities, and Thomson (1926, p. 150) stated that the mean around which variation occurs differs between localities, suggestive of hybridism, according to him. The measured mean for each locality does in fact differ as well – mean length and width at Devil's Bridge are 34.5 mm. and 29.1 mm. respectively; at Deborah, 36.3 mm. and 30.1 mm. respectively (derived from data supplied in Appendix). It is considered here that the Deborah and Devil's Bridge material represent two distinct variant populations of the same species. The statistical differences observed are interpreted to be a result of inter-population variation. Graph 14 demonstrates the essential identicalness of the two populations when both are

graphed on a length versus width scattergram. Due to poor preservation, significant induration and presence of a hard limonitic cement in the Allan Collection (University of Canterbury) and additionally collected specimens, brachiopod samples from Landon Creek, the type locality for *Pachymagas hectori*, could not be analysed statistically.

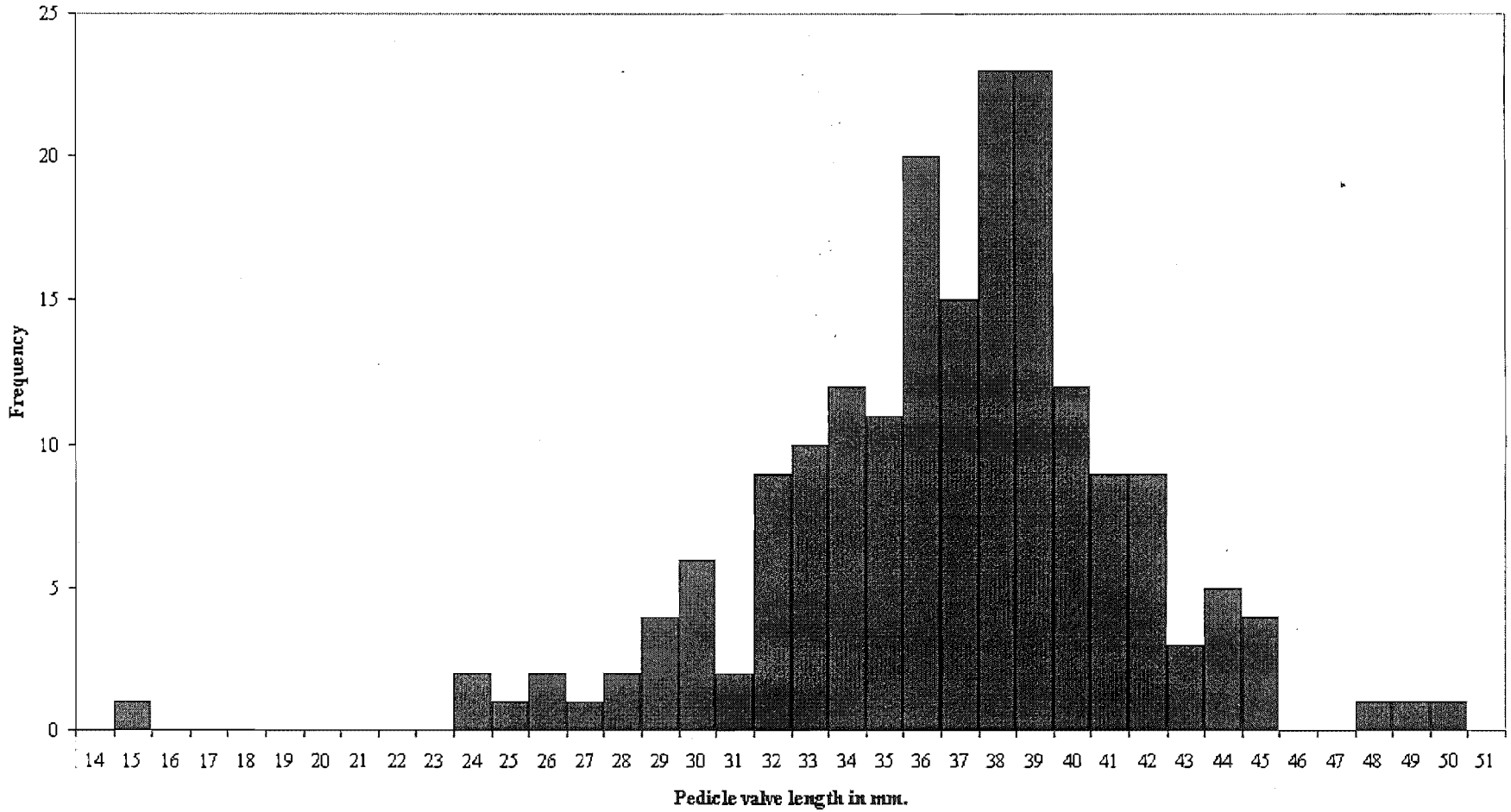
Thomson (1915) made distinction between the advanced (see discussion of this terminology in section 2.1) cardinal process of species such as *Pachymagas parki* (*Waitakia parki* – section 3.10) and the more primitive cardinal process of species such as *haasti*. This study found that such a distinction, at least between *parki* and *haasti* is not as clear-cut as advanced and primitive (respectively). *Waitakia haasti* has proven to have a moderately advanced cardinal process comparable to that possessed by *parki,* though some adults retain the primitive pyramidal process of juveniles. The two species do, however, differ in the *consistency* with which they display a cardinal process in an advanced state of development. In *W. parki* the cardinal process is consistently of a moderately advanced type, while the process of *W. haasti* is not consistently moderately advanced, many specimens rather having a primitive process.

The shape and size of the cardinal process and nature of the anterior portion of the hinge-trough was seen to vary considerably in both *haasti* and *parki*, and in all other species of *Waitakia* where a sufficient number of interiors were available to give a representative sampling. Figures 52 and 53 illustrate typical variation seen in the cardinal process of *W. haasti* – fig. 53b demonstrating presence of a primitive cardinal process in the adult shell and 52c a moderately advanced process. Figures 52d and 53a demonstrate swelling together of the crural bases and confinement of the dorsal pedicle adjustor muscle attachment sites to the posterior of the hinge-trough.

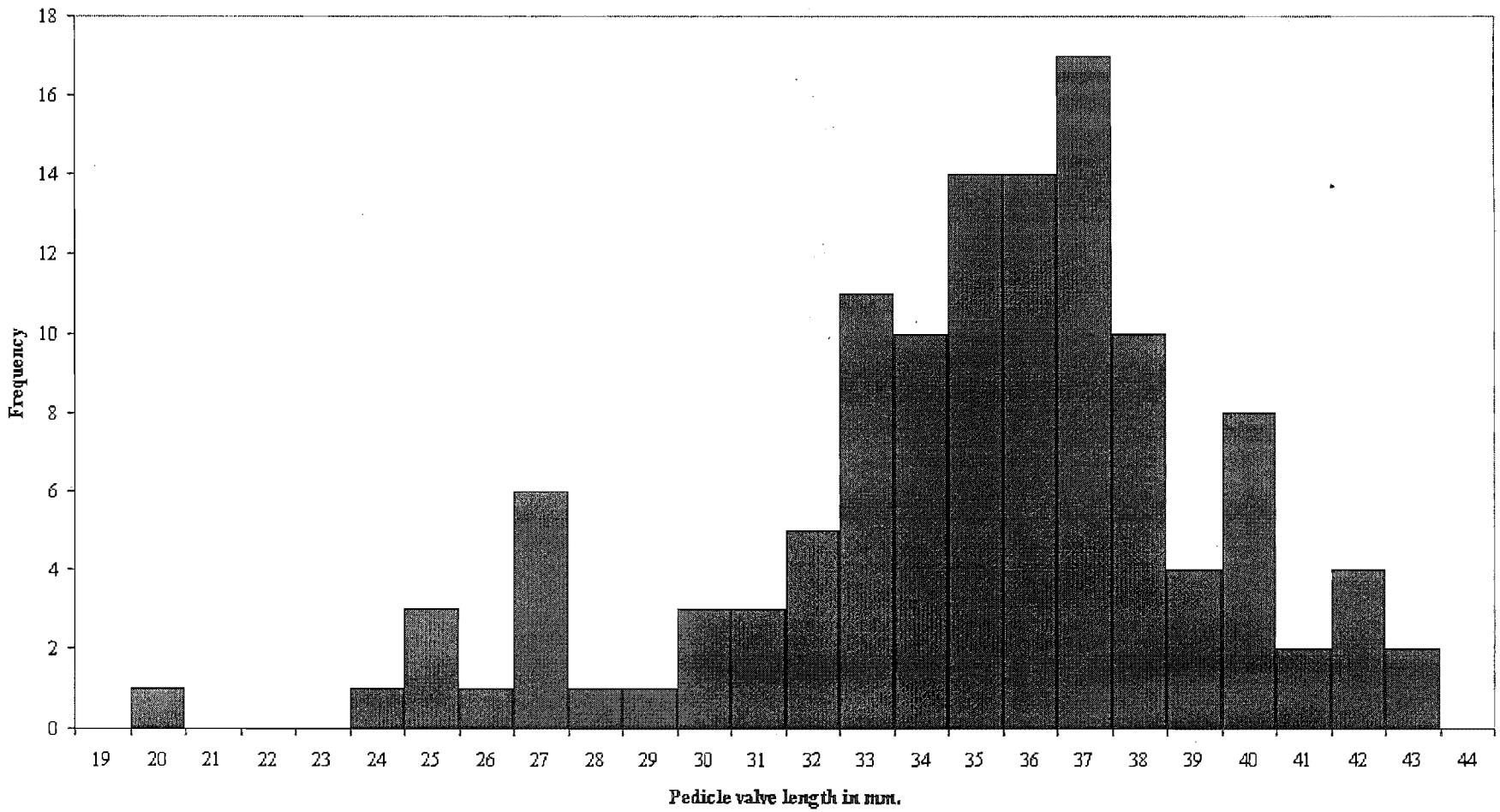
Graph 9: Histogram showing shell length at which maximum shell width was measured from Devil's Bridge



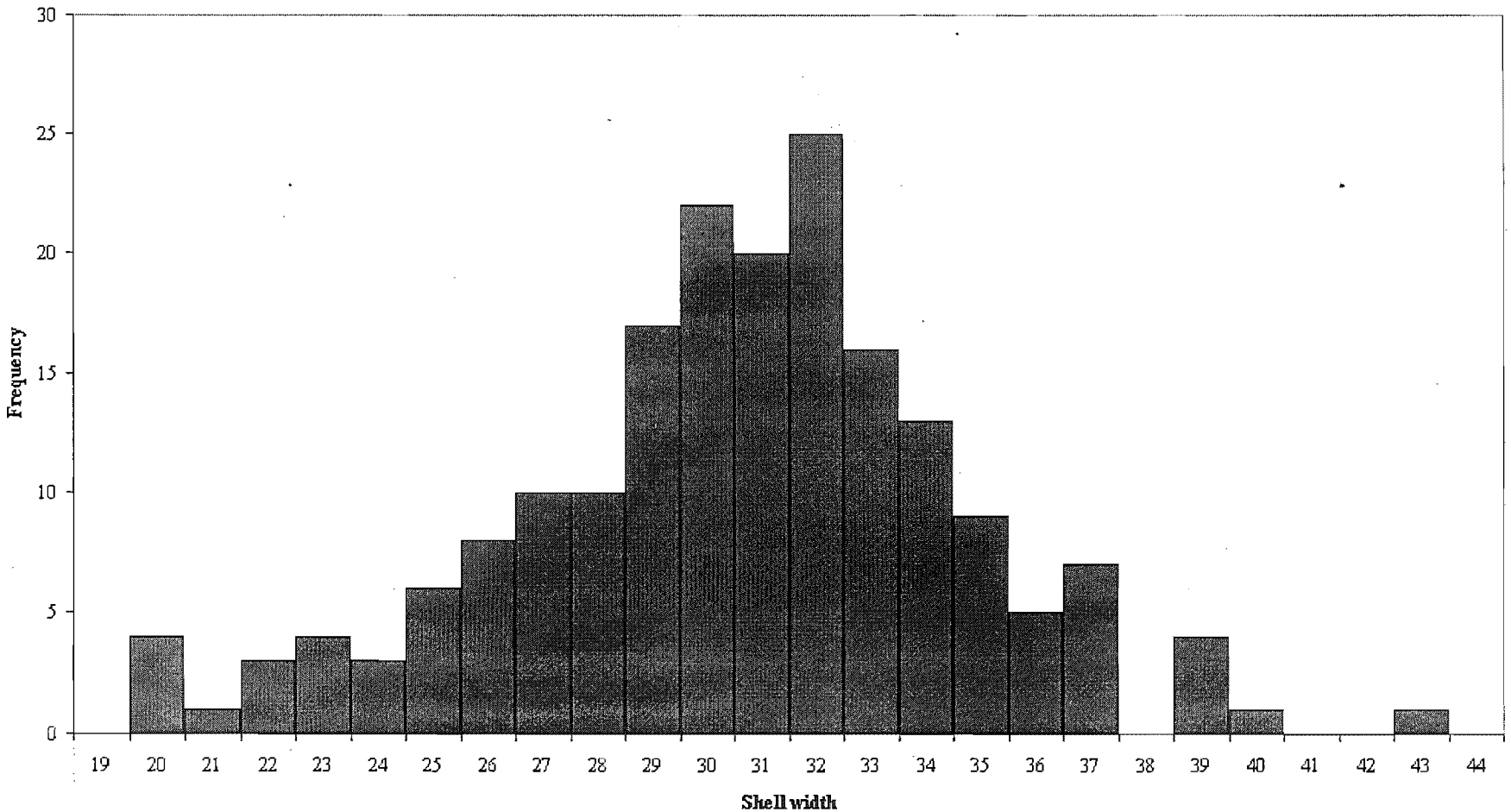
Graph 10: Histogram of pedicle valve length for Waitakia haasti from Deborah



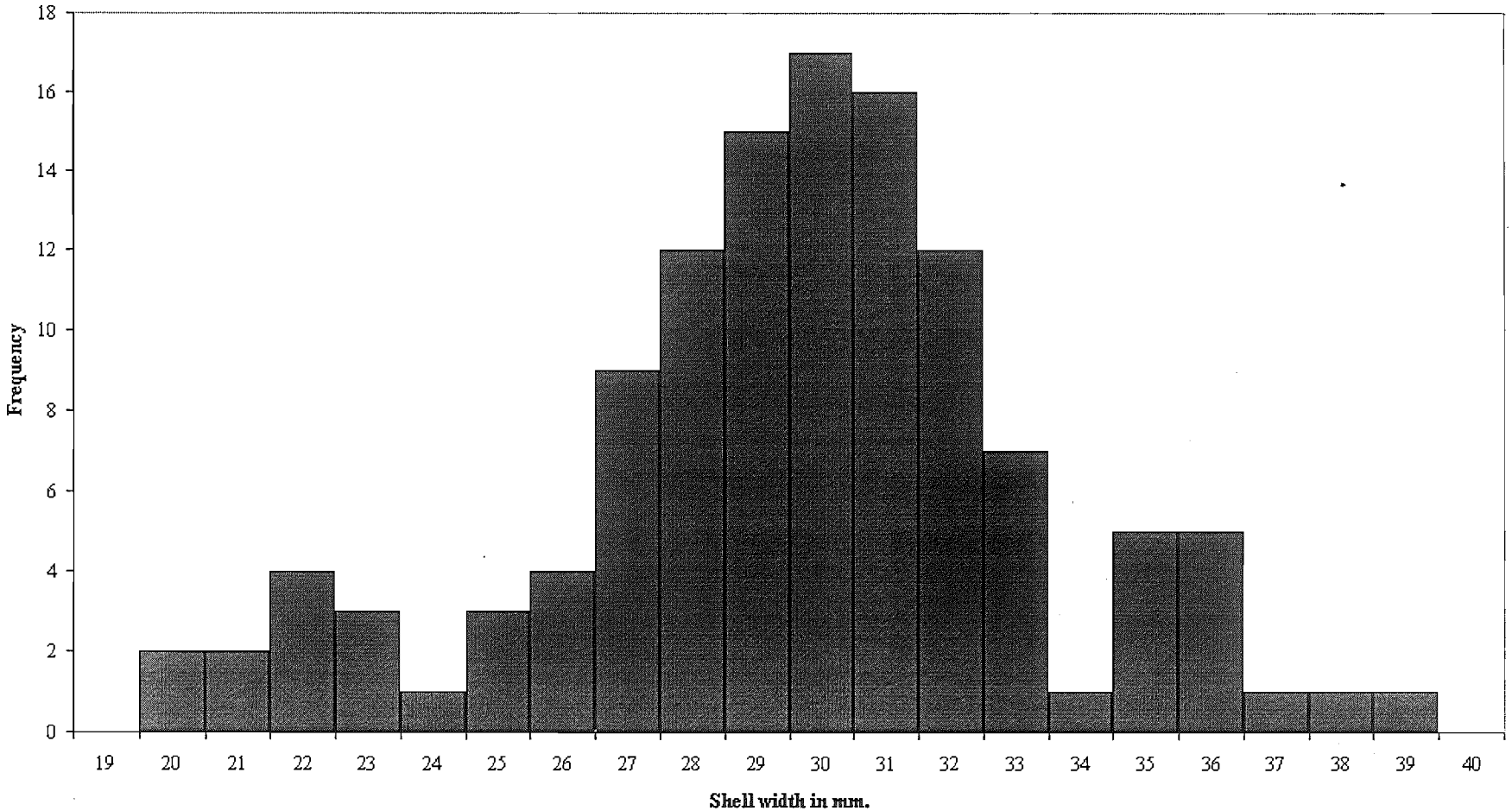
Graph 11: Histogram of pedicle valve length for Waitakia haasti from Devil's Bridge



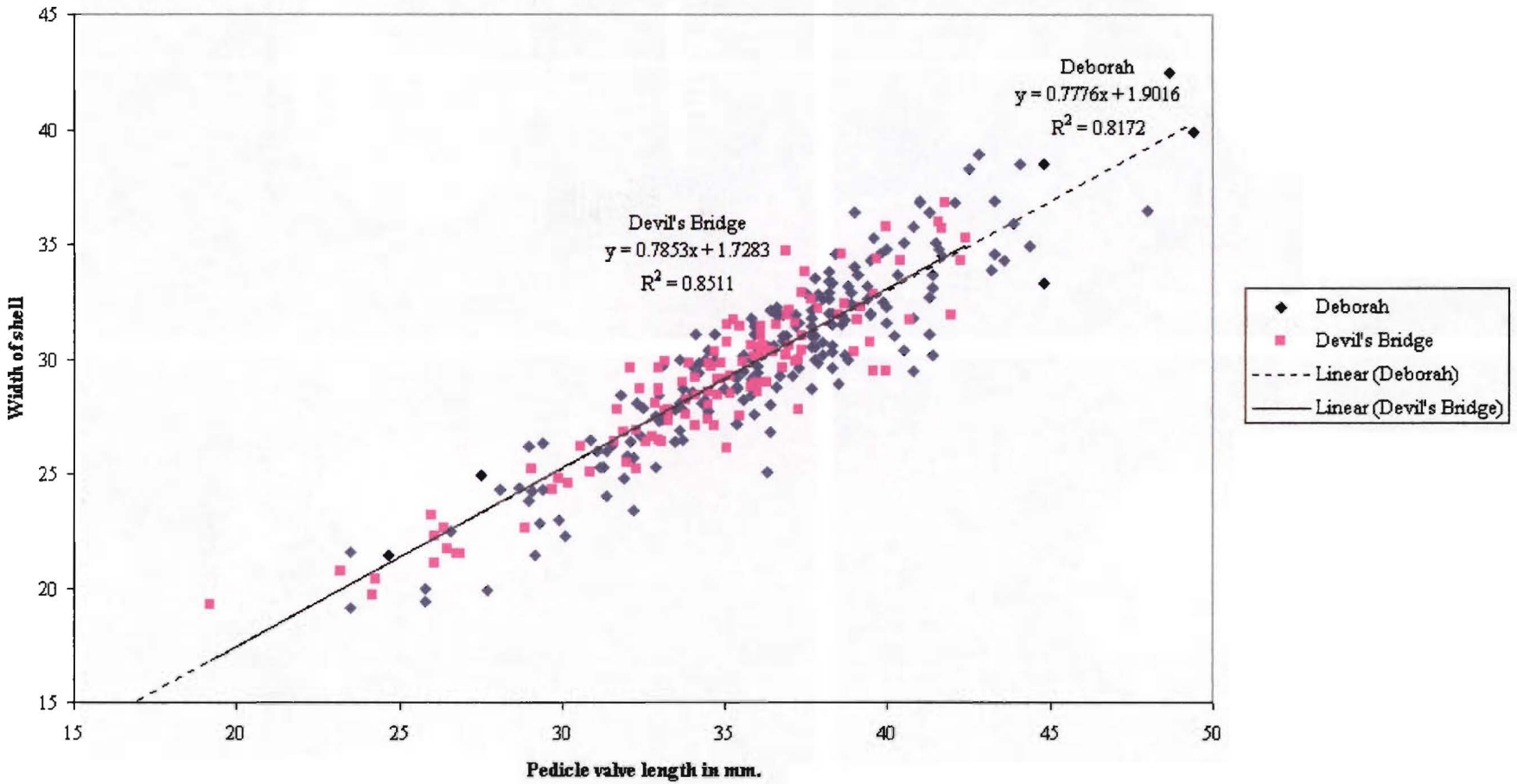
Graph 12: Histogram of shell width for Waitakia haasti from Deborah



Graph 13: Histogram of shell width for Waitakia haasti from Devil's Bridge



Graph 14: Pedicle valve length vs. Width of shell for Waiparia haasti from Deborah and Devil's Bridge (four outliers have been removed)



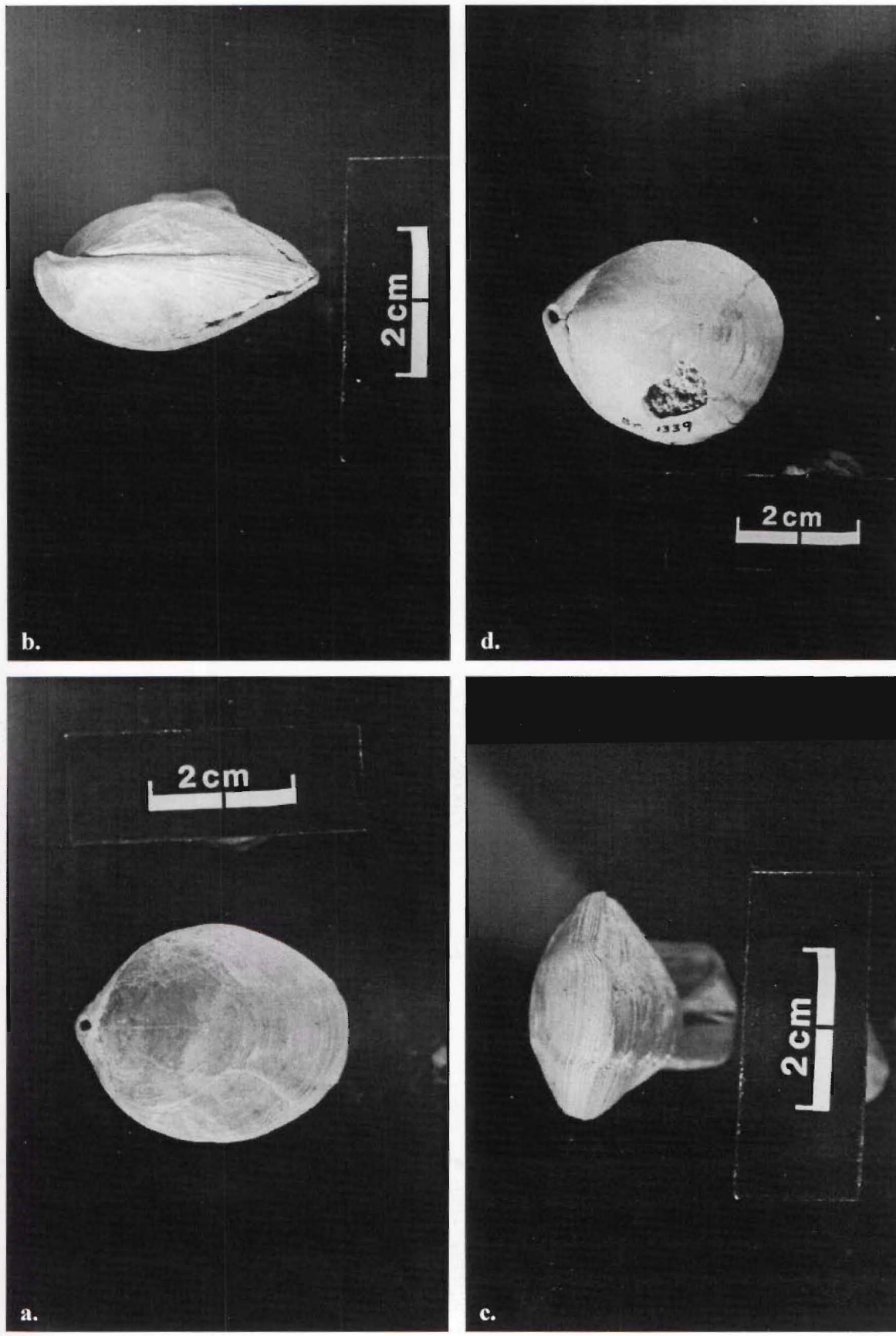


Figure 50. Holotypes of *Pachymagas haasti* (**a**, **b**, **c**: Br 124) and *P. hectori* (**d**: Br 1339).

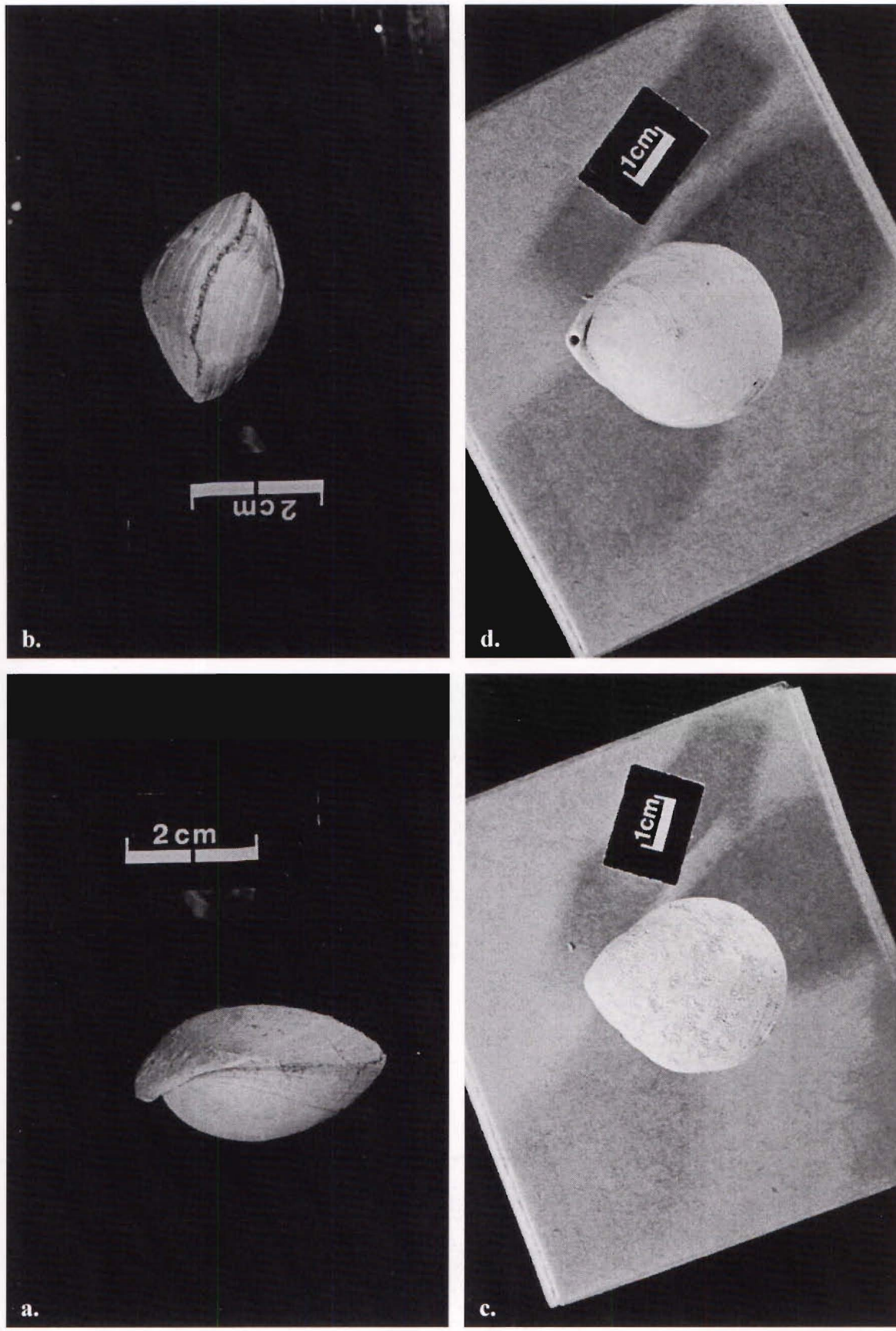


Figure 51. Holotype of *Pachymagas hectori* (**a**, **b**: Br 1339) and ventral and dorsal valves of *Waitakia haasti* (**c**, **d**: Allan Colln. 26974; Deborah).

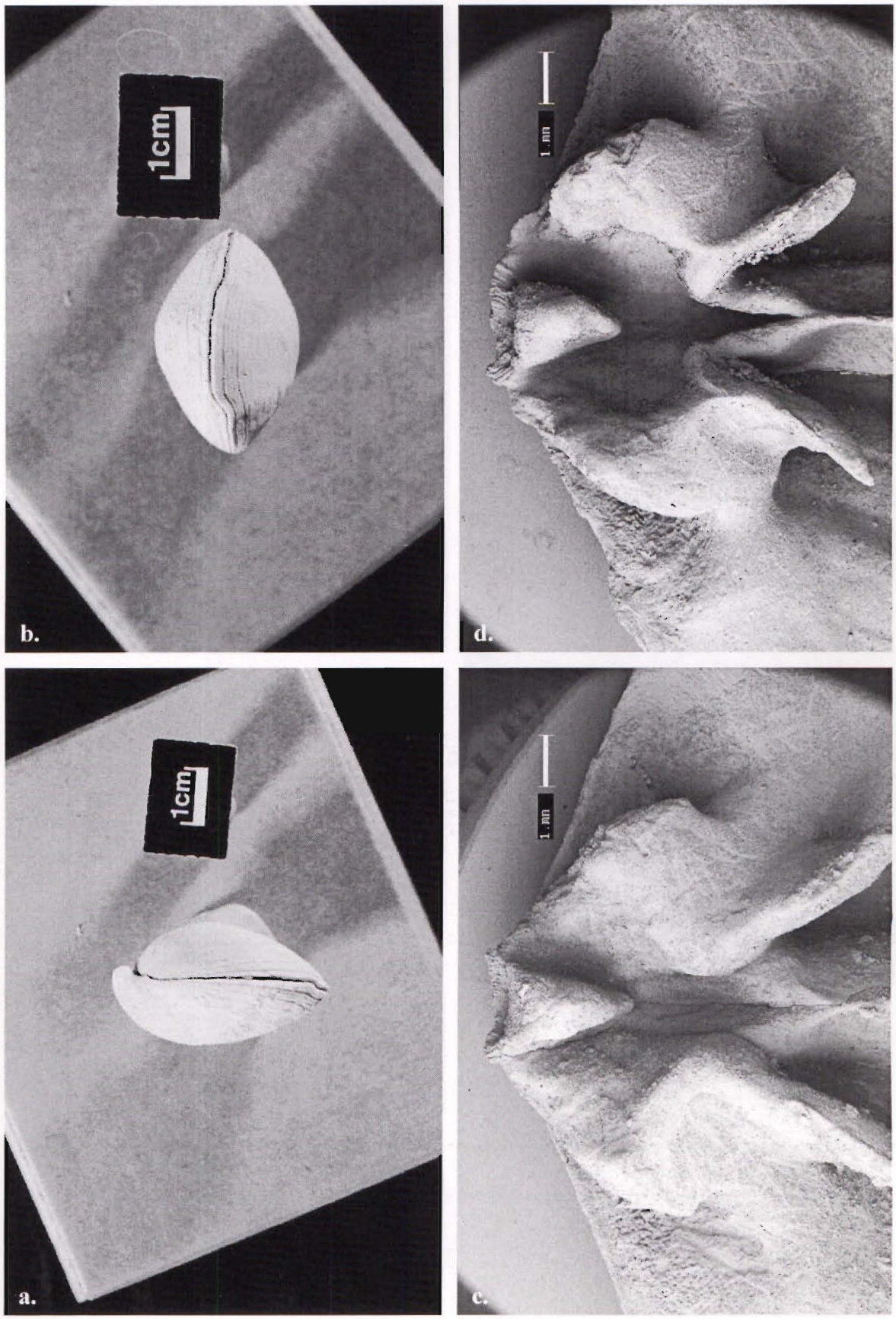


Figure 52. Exteriors (**a**, **b**: Allan Colln. 26974; Deborah) and variable dorsal interiors (**c**: UCM 2000; Deborah; **d**: UCM 2001; Devil's Bridge) of *Waitakia haasti*.

Figure 53. Dorsal interiors of *Waitakia haasti* (**a**: UCM 2002; Deborah; **b**: UCM 2003; Devil's Bridge; **c**: 2004; Deborah) demonstrating variation (see also fig. 52).

3.9 *Waitakia marshalli* (Andrew, 1906)

SYNONYMY:

Magellania insolita Hutton, 1905 (in part), p. 476, pl. XLV, fig. 5 (not the species of Tate, 1880)
Magellania triangularis Hutton, 1905, p. 477 (not the species of Hutton 1873b)
Magellania marshalli Andrew, 1906, p. 456, pl. IV, figs. 3a-b
Pachymagas huttoni Thomson, 1915, p. 403, text fig. 2c
Pachymagas marshalli Thomson, 1920, p. 375, text fig. 7
Pachymagas clarkei Thomson, 1920, p. 376-377, pl. XXVI, figs. 3-6
Pachymagas huttoni Thomson, 1920, p. 379-380, pl. XXVI, figs. 7-9 (first figure of the holotype)
Pachymagas marshalli Thomson, 1926, p. 150
Pachymagas huttoni Thomson, 1927, p. 89, text fig. 29c
Pachymagas huttoni Allan, 1937a, p. 120
"*Pachymagas*" *huttoni* Allan, 1960, p. 240, 264 (stratigraphic range)
"*Pachymagas*" *clarkei* Allan, 1960, p. 242, 263 (stratigraphic range)
"*Pachymagas*" *marshalli* Allan, 1960, p. 252, 264 (stratigraphic range)
Pachymagas clarkei Keyes, 1971, p. 81
"*Pachymagas*" *huttoni* Dawson, 1990, p. 66-67
"*Pachymagas*" *marshalli* Dawson, 1990a, p. 68

TYPE LOCALITY: Milburn Limestone, Milburn Quarry, South Otago.

TYPE MATERIAL: Holotype (C.03.31) in Otago Museum, Dunedin. Location of holotype of *Pachymagas huttoni* Thomson 1915 unknown. Paratype (B48) of *P. huttoni* in Canterbury Museum, Christchurch. Holotype (Br 127) of *Pachymagas clarkei* Thomson 1920 in the National Museum of New Zealand, Wellington. Paratypes in the National Museum of New Zealand (fig. 6 of Thomson 1920, pl. XXVI) not located by Keyes (1971).

(Source: Dawson 1990a)

OCCURRENCE: Milburn Limestone {South Otago}, at: Milburn Quarry; Otekaike Limestone {North Otago}, at: Brothers Stream, Earthquakes, Landon Creek, Maerewhenua River, Meyers Pass, Nicholls Road, Otekaike, Trig Z, Kokoamu Bluff, {South Canterbury}, at: Haugh's Quarry, Fossil Point (Ashburton River), Blands Bluff (and in interbedded tuff layers), Cave, Squires Farm; Berrydale Greensand {South Canterbury}, at: Curiosity Shop; Bluecliffs siltstone {South Canterbury}, at: Bluecliffs; Weka Pass Stone {North Canterbury}, at: Onepunga; Whiterock Limestone {North Canterbury}, at: Onepunga, Whiterock Quarry; Caversham Sandstone {South Otago}, at: Green Island.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (413-454 Curiosity Shop) ; (1824-1834 Onepunga) ; (26681-26684 Green Island) ; (27695-27739 Maerewhenua River) ; (27740-27761 Otekaike Special School) ; (27766-27771 Otekaike Special School) ; (27986-27989 Blands Bluff) ; (27990-27998 Fossil Point) ; (28038-28048 Bluecliffs) ; (28057 Curiosity Shop) ; (28058 Curiosity Shop) ; (28059 Curiosity Shop) ; (28115-28124 Squire's Farm) ; (28617-28638 Onepunga) ; (28640-28643 Onepunga). Unnumbered collections, University of Canterbury, Department of Geological Sciences: (Meyers Pass (box): S. E. Belliss MSc. Thesis Collection) ; (Brothers Stream (bag), Haugh's Quarry (bag), Whiterock Quarry (bag), Meyers Pass (bag): D. I. MacKinnon Collection) ; (Nicholls Road (bag), Kokoamu Bluff (2 bags): S. Fryer MSc. Thesis Collection) ; (Milburn Quarry (four topotypes): collected by R. S. Allan).

AGE/RANGE: Waitakian – Otaian

FIGURES: 55-64

DESCRIPTION: Medium to large, smooth, biconvex shell displaying numerous faint growth-lines; shell suborbicular to broadly suborbicular, often demonstrating marked inflation of the ventral valve, which is strongly carinated posteriorly; wide cardinal margin almost straight to gently curved; anterior commissure weakly to moderately broadly unisulcate. Beak compressed, obtuse, erect, attrite; large circular mesothyrid foramen ranging to permesothyrid in some specimens; beak ridges fairly well defined; gently convex cardinal area with conjunct deltidial plates that are short due to the compressed beak. Median septum relatively thickened, extending anteriorly about one-third of valve length, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped hinge-trough with, normally, shallowly inclined walls; crural bases fused to the thickened inner socket ridges. Cardinal process consisting of roughened myophore is usually small and pyramidal, confined to the posterior portion of the hinge-trough, but can develop a boss-like anterior swelling with growth that projects ventrally; the cardinal process occupies the posterior one-third of the hinge-trough, often tapering anteriorly to occupy up to one-half of the hinge-trough; wing-like projections of myophore develop posteriorly. Dorsal adductor muscle scars are large and distinct, terminating anteriorly at approximately the termination point of the median septum – at one-third the length of the valve. The large muscle-field scars of the ventral valve are impressed such as to produce a low median ridge in the valve floor between the scars. The teeth are large and sturdy, and are perched on swollen bases, which are grooved to accommodate the swollen inner socket ridges. Adult loop trabecular, the transverse connecting band attenuated.

DISCUSSION: "It is a curious fact that in Waitakian strata in the Waitaki Valley *P. huttoni* Thomson is never accompanied by other species of brachiopods." (Allan

1960, p. 240). In fact, other species of brachiopod are recorded as occurring with *P. huttoni* (*Waitakia marshalli*) by Belliss (1978) in the Waitaki and Hakataramea Valleys of North Otago, though *W. marshalli* is the dominant species in all of these localities. Belliss indicates occurrence of *P. huttoni* with *Aethia* sp. at Meyers Pass and Awamoko, and with *Terebratulina* sp. in the Maerewhenua River section.

Allan's above observation must be explained as occupation by *marshalli* of a habitat unfavoured for occupation by its contemporaries. The species is found in the Waitaki and Hakataramea Valleys in the Otekaike Limestone, or its correlatives. Allan (1957) stated that his collections of brachiopods from the limestone were made before Gage's (1957) subdivision of it into four Members, and stated that new collecting was therefore necessary. Belliss (1978) did this in part, her paleoecological study on the Otekaike Limestone indicating significant ecological differences between the lower Maerewhenua Member and upper Miller and Waitoura Marl Members (N.B. Belliss' Members don't exactly correspond to Gage's originally established members – reference should be made to figure 54 which compares the two schemes; Belliss' scheme is used in this discussion); differences such that a comparison of separate collections of *W. marshalli* from the Maerewhenua and Miller Members would obviously be desirable. According to Belliss' paleoecological reconstructions, the fauna of the Maerewhenua Member represents a "predominantly clear water epifaunal filter-feeding community on the sea-floor...while the sediment supported a rich deposit-feeding spatangoid fauna and a wide variety of soft-bodied burrowers" (Belliss 1978, p. 296). In contrast, the fauna of the Miller and Waitoura Marl Members represents a "temperate-subtropical water community dominated by shallow infaunal, suspension feeding bivalves and epifaunal scavenging and predatory

gastropods" (Belliss 1978, p. 1). The Maerewhenua Member originally would have presented a very soft substrate to the potential brachiopod occupant, and this is very probably the reason that the Member was only colonised to any extent by *W. marshalli*. *Waitakia marshalli* is suborbicular in shape, and typically the valves are inflated; this shape probably helped to distribute the weight of the animal evenly across the substrate, enabling it to maintain a stable position on a soft substrate. In this respect it is illuminating that *W. marshalli* is associated at Balfour Quarry, Southland, with *Pycnozygus triangularis* (section 3.12), a brachiopod that displays a marked exterior similarity to *marshalli*. This similarity of external form probably represents similar adaptation for support on unconsolidated substrata.

Waitakia marshalli is interpreted in this study to have had a free-lying habit (in the sense of Richardson 1981c); interior characteristics observed of some specimens requires discussion in this context. The muscle scars associated with the dorsal pedicle adjustors in specimens from Brothers Stream and Haugh's Quarry are large and well expressed, and extend anteriorly to the juncture of the bifurcated septum (fig. 59b). Richardson (1981a) has stated that, where the dorsal pedicle adjustor muscles are long, the rotary arc may be wide. Thus, examination of the dorsal pedicle adjustor muscle scars leads to the conclusion that the dorsal pedicle adjustors must have been very active, and probably enabled significant rotation. This being so, *W. marshalli* must have had a significant 'anchor' – a large fragment of echinoid test or brachiopod valve, as only large planar pieces would have the correct geometry to allow for rotation of the brachiopod rather than rotation of the pedicle attachment site itself within the soft sediment. Specimens from all other localities examined in this study do not possess dorsal pedicle adjustor muscle scars that are as well developed as

specimens from Brothers Stream and Haugh's Quarry. It is therefore considered that at all these other localities *P. huttoni* sat passively, and did not actively rotate on the sediment. The reason *W. marshalli* might have actively rotated is probably related to nutrition – active orientation to nutritious currents. It does not appear that the rotary action could have acted to extricate the animal from rapidly deposited sediment (c.f. *Magadinella mineuri*, Richardson 1987).

Examination of material from the Allan Collection at the University of Canterbury and of material collected during the course of this study demonstrates that *W. marshalli* maintains a consistent morphology between the Members of the Otekaike Limestone throughout the Waitaki Valley, though it was noted that specimens collected from the section at Nicholls Road (see Gage 1957, p. 79) differed slightly (fig. 58). These specimens seem to be rather compressed and disc-like, not displaying the typical inflation of *marshalli*, nor the carination. In some specimens from this locality the beak is suberect rather than erect, with a fairly small to medium sized foramen. In these respects the species resembles the typical disc-like form found at Milburn Quarry (including the holotype, C.03.31). However, it should be noted that four unnumbered topotypes of *marshalli* collected by R. S. Allan from Milburn Quarry (University of Canterbury), though crushed, are the typical inflated, strongly carinate form. Considering that these disc-like and inflated representatives are found within the same Formations and Members, it is speculated that the disc-like form sometimes found represents an ecophenotype, occurring as small, local ecophenotypic sub-populations.

Other localities where it is considered that the populations present are ecophenotypic are Blands Bluff, Fossil Point, Curiosity Shop, Onepunga, and

Whiterock Quarry. At both Blands Bluff and Fossil Point *W. marshalli* occurs in Otekaike Limestone interbedded with tuff bodies of the Brothers volcanics (Field & Browne 1986). Here the species range from disc-like to moderately inflated, have prominent ventral palintropes and suberect beaks that are produced (fig. 64). Examination of two specimens (Allan Colln. 27993 and 27997 (fig. 64c)) which were partially excavated reveals that the cardinal process is large, the anterior boss projecting ventrally from the floor of the hinge-trough. The hinge-trough walls are steep, the anterior portion of the bifurcated septum closing. All these features help to weight the shell posteriorly, perhaps helping to elevate the commissure further off of the substrate. It must be noted that the consistency of the interior characteristics was not able to be determined due to small available sample size (as is shown in discussion of *Waitakia haasti* (q.v.), the cardinalia of the genus has a highly variable morphology). At Curiosity Shop *W. marshalli* occurs in the Berrydale Greensand (fig. 63c, d), and is found to be relatively small. It is possible that individuals here grew at a slower rate due to unsuitable or stressed environmental conditions, reaching a smaller adult size and being less well developed overall (interiorly the specimens are simple, somewhat resembling the juveniles from other localities). The fact that the population occurs in a greensand rather than a limestone demonstrates a change in gross environment, a change inducing an ecophenotypic response in *W. marshalli.* Very rarely specimens from Curiosity Shop reach larger, more typical sizes, as illustrated in figure 63 (a, b).

The ecophenotype found in the Whiterock Limestone at Onepunga and Whiterock Quarry (fig. 62) is very interesting because both interiorly and exteriorly it resembles *W. haasti* significantly, though some specimens retain, at least, the exterior

form of typical *marshalli*. *Waiparia haasti* is found in medium glauconitic bryozoan greensands in Oamaru, while *marshalli* at Onepunga and Whiterock Quarry is found in a coarse bryozoan limestone. At both these localities the brachiopods are Otaian in age. These similarities of morphology and age lead to speculation about the phylogenetic relationship between *W. haasti* and *W. marshalli*, but this is covered in section 4.0, and is not further discussed here. McCulloch (1981) suggested that specimens from the Whiterock Limestone were commonly aligned in life, the brachiopods being preserved in a life position in the limestone. She interpreted the limestone as being deposited in a "clear water environment with moderate current activity and a low sedimentation rate" (McCulloch 1981, p. 48). The common alignment of *W. marshalli* taken to indicate a constant current direction by McCulloch. This fits with the morphology of the cardinalia in the specimens from this limestone; evidence for strong rotary movement of the shell, namely large dorsal pedicle adjustor muscle scars, is absent. The brachiopod would not have had to actively orient itself to a changing current direction, hence the lack of large dorsal pedicle adjustor muscle scars.

At localities where specimens of *W. marshalli* are large (e.g. Meyers Pass, Otekaike Special School), the beak is invariably compressed, burying the deltidial plates, and possessing a large foramen. Interiorly these large inflated specimens display a large, well developed cardinal process, the anterior boss rising high off of the floor of the hinge-trough (fig. 61).

Graph 15 demonstrates graphically that *W. marshalli* is differentiated from most other species of the genera by its smaller length to width ratio. Comparison is made between *W. marshalli* from Maerewhenua River and *W. haasti* from Deborah.

Waiparia haasti was chosen for comparison because it has the 'typical' ovate or tear-drop shape of the genus, and because specimens of the species have a similar mean length.

Graph 16 displays a histogram for *W. marshalli* from Maerewhenua River (Maerewhenua Member of the Otekaike Limestone), and has a notable bimodal distribution. This is interesting, as other material such as *W. haasti* from Deborah, when similarly graphed, display only one mode. These modes *perhaps* correspond with the modes of the original living population (representing periods of recruitment), the fossil material therefore considered to be *in situ*. This might appear doubtful because of the fact that no juveniles are represented in the sample, the smallest representative being some 25 mm. in length. However, the absence of juveniles from an *in situ* accumulation might be due primarily to a low juvenile mortality rate. On the other hand, Belliss (1978, p. 221) provided histograms for material collected from the Meyers Pass Limestone (a correlative of the Maerewhenua Member) which suggest a high juvenile mortality rate for the population there. As the histogram for the Maerewhenua River material incorporates data from only 39 individual brachiopods it could well be the case that the bimodality is spurious. The R. S. Allan brachiopod collection, from which the Maerewhenua River material was measured, is probably not strictly statistically representative of material found at the localities, as Allan seemed to collect only the well preserved, aesthetically appealing material. This being the case, it is not undertaken to discuss *in detail* what these statistical techniques may or may not tell us. Having said this, the point to make is that where a unimodal distribution of length measures for *Waitakia* is found, the material may have undergone at least local transportation after death.

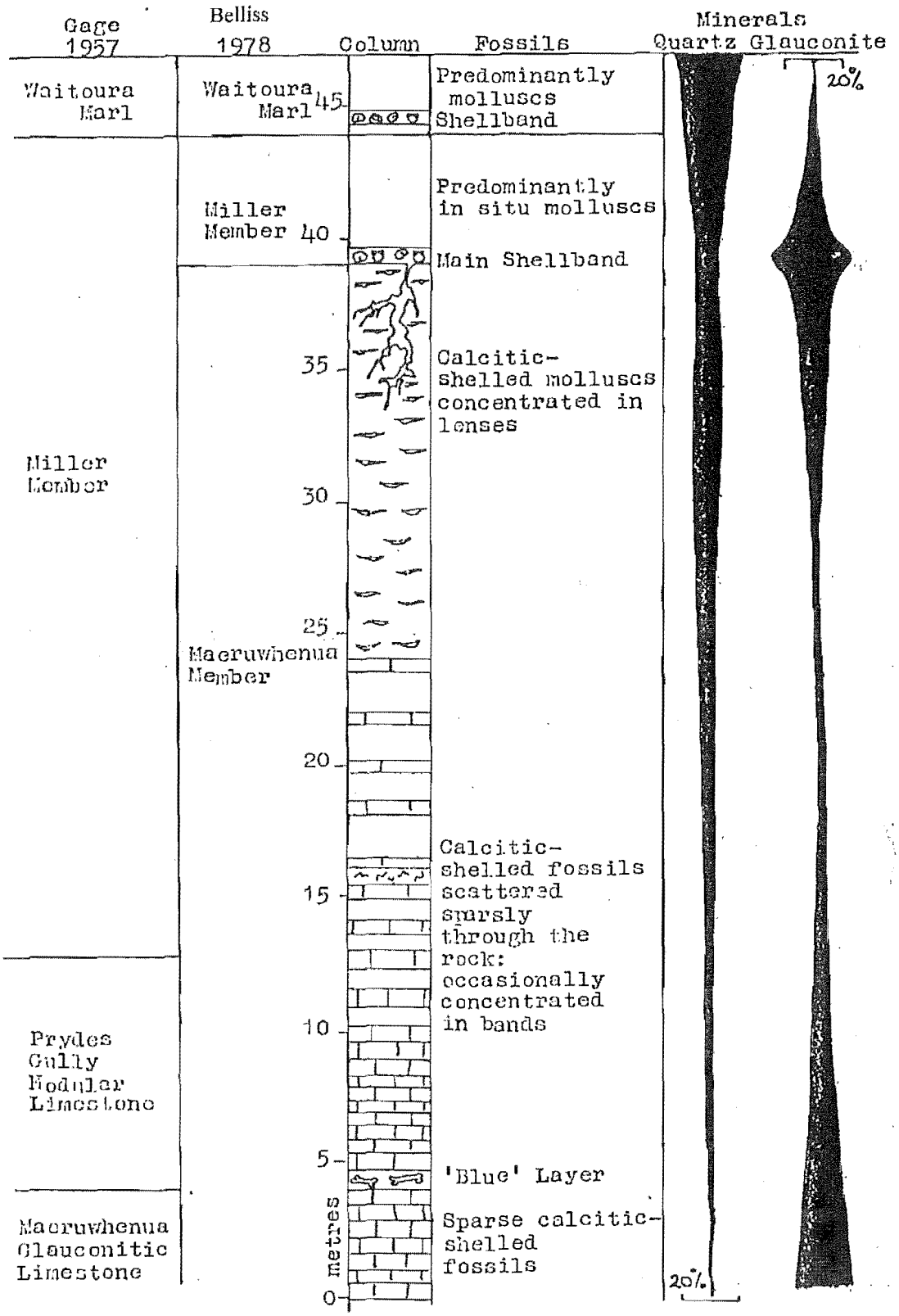
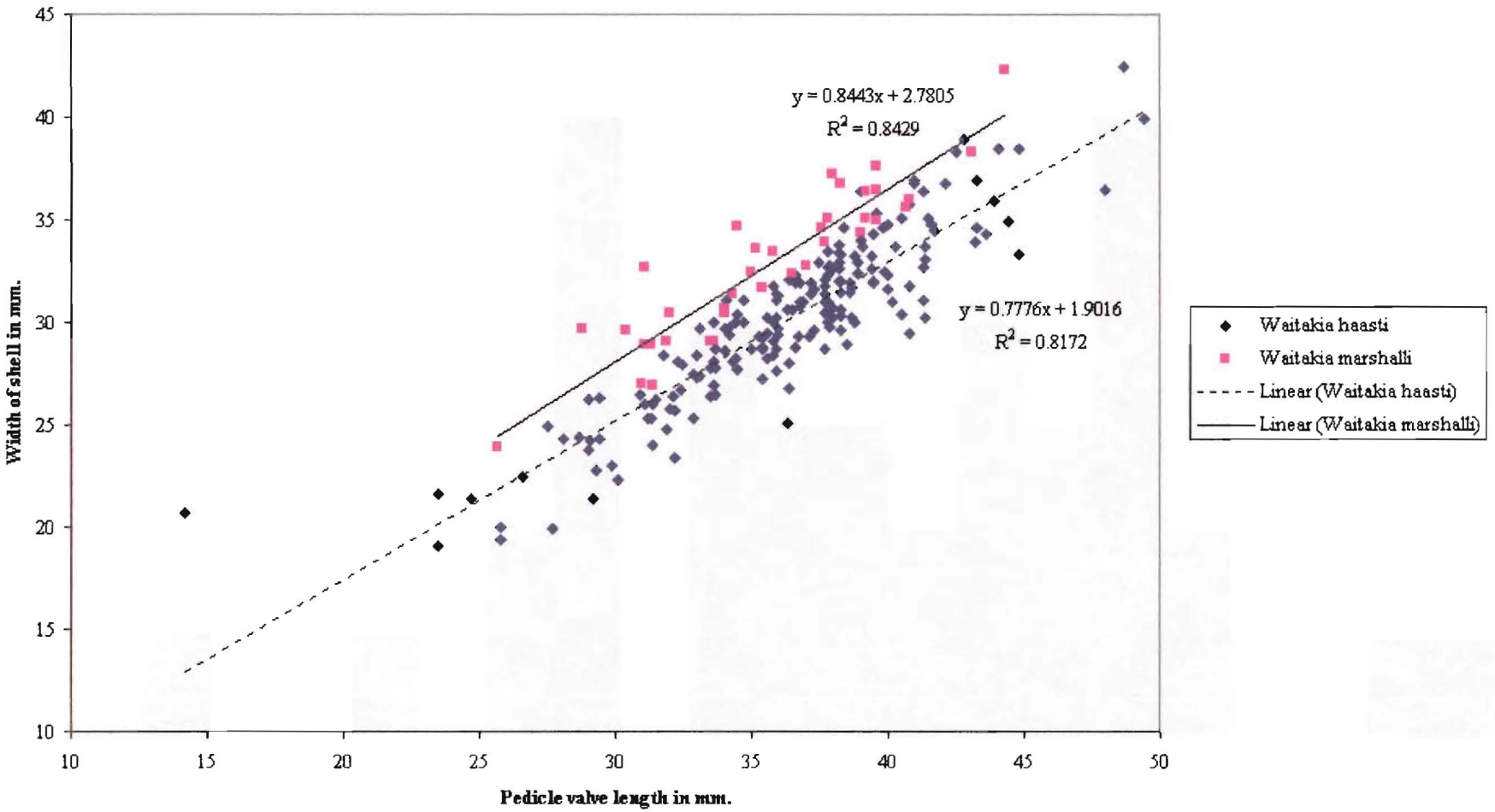
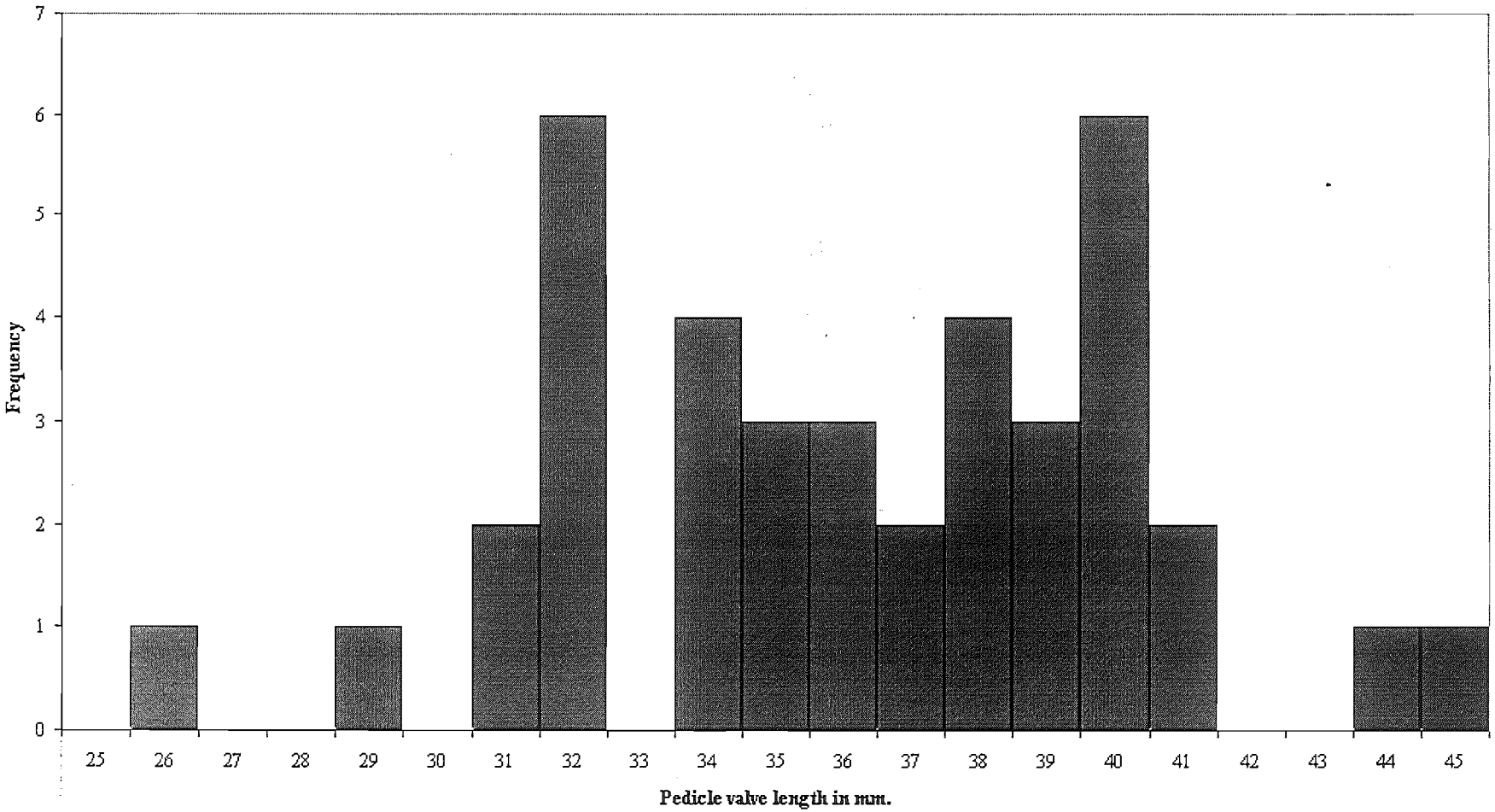


Figure 54. Stylised stratigraphic column for the Otekaike Limestone from the south bank of the Waitaki River. The figure demonstrates the different schemes of subdivision adopted by Gage and by Belliss. Note that Belliss incorporated Gage's Prydes Gully Member and most of his Miller Member within her Maerewhenua Member. (From Belliss 1978)

Graph 15: Pedicle vavle length vs. Width of shell for Waitakia haasti and Waitakia marshalli



Graph 16: Histogram of pedicle valve length for Waitakia marshalli from Maerewhenua River



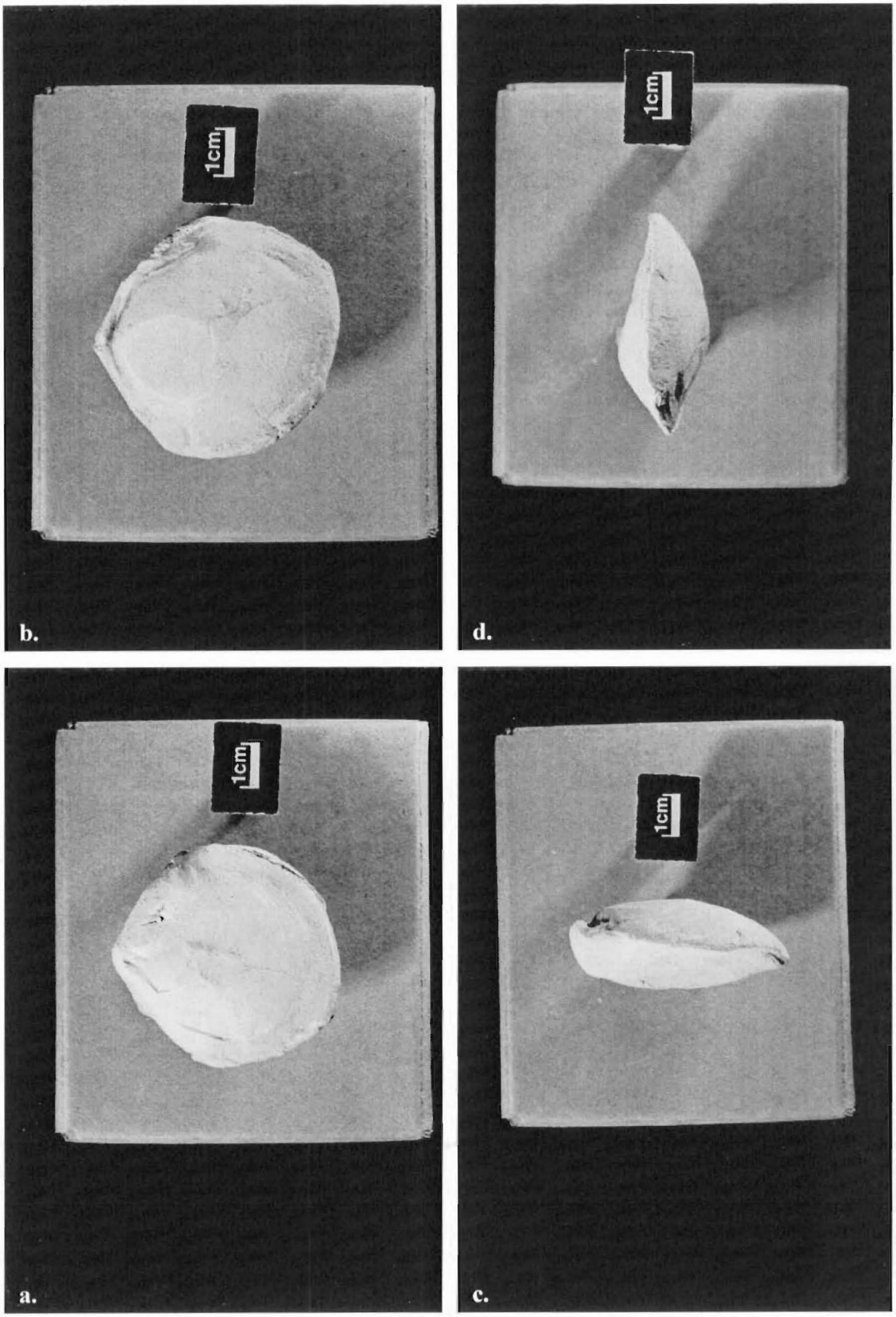


Figure 55. Holotype (C.03.31) of *Pachymagas marshalli*.

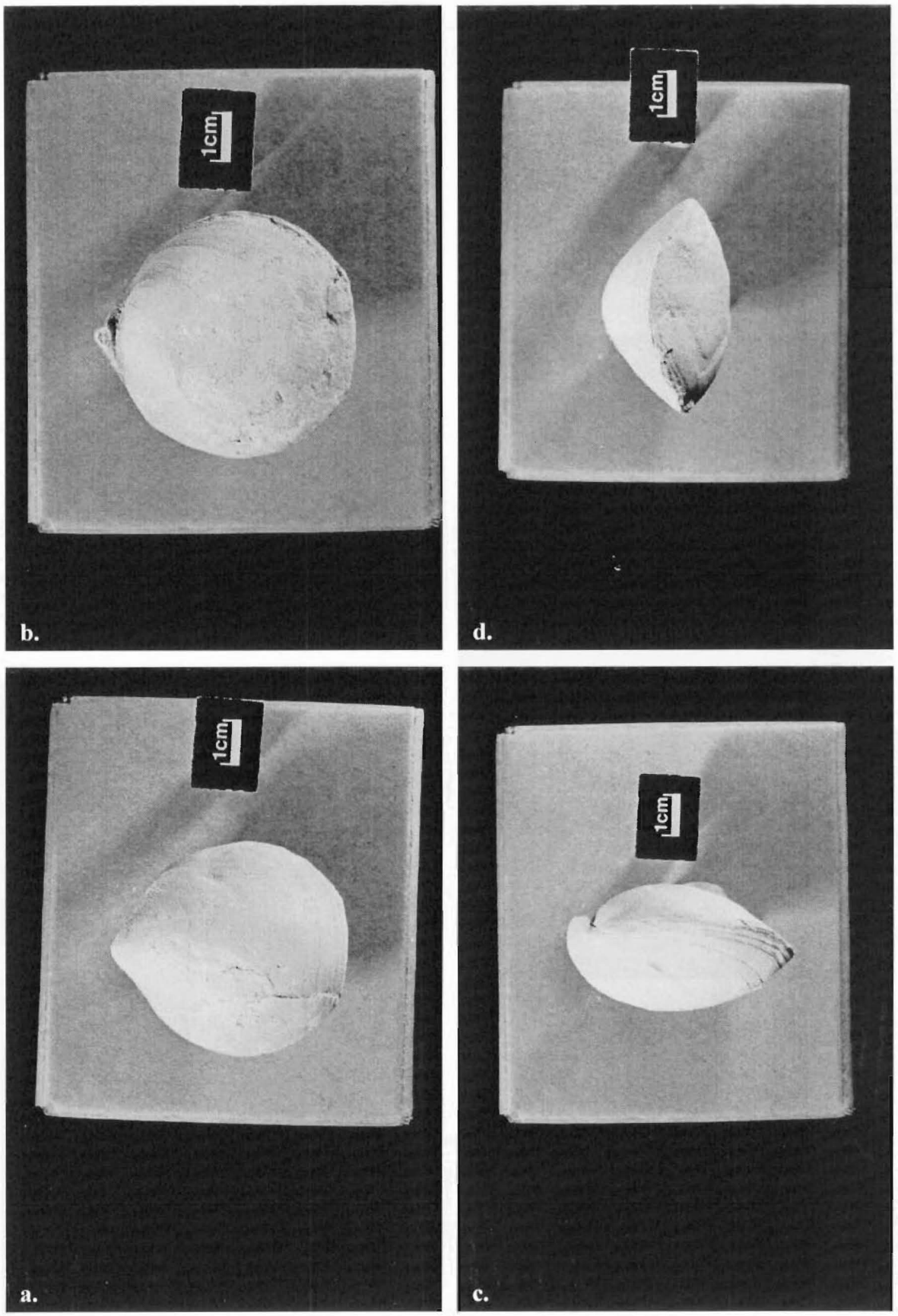


Figure 56. Paratype (B48) of *Pachymagas huttoni*.

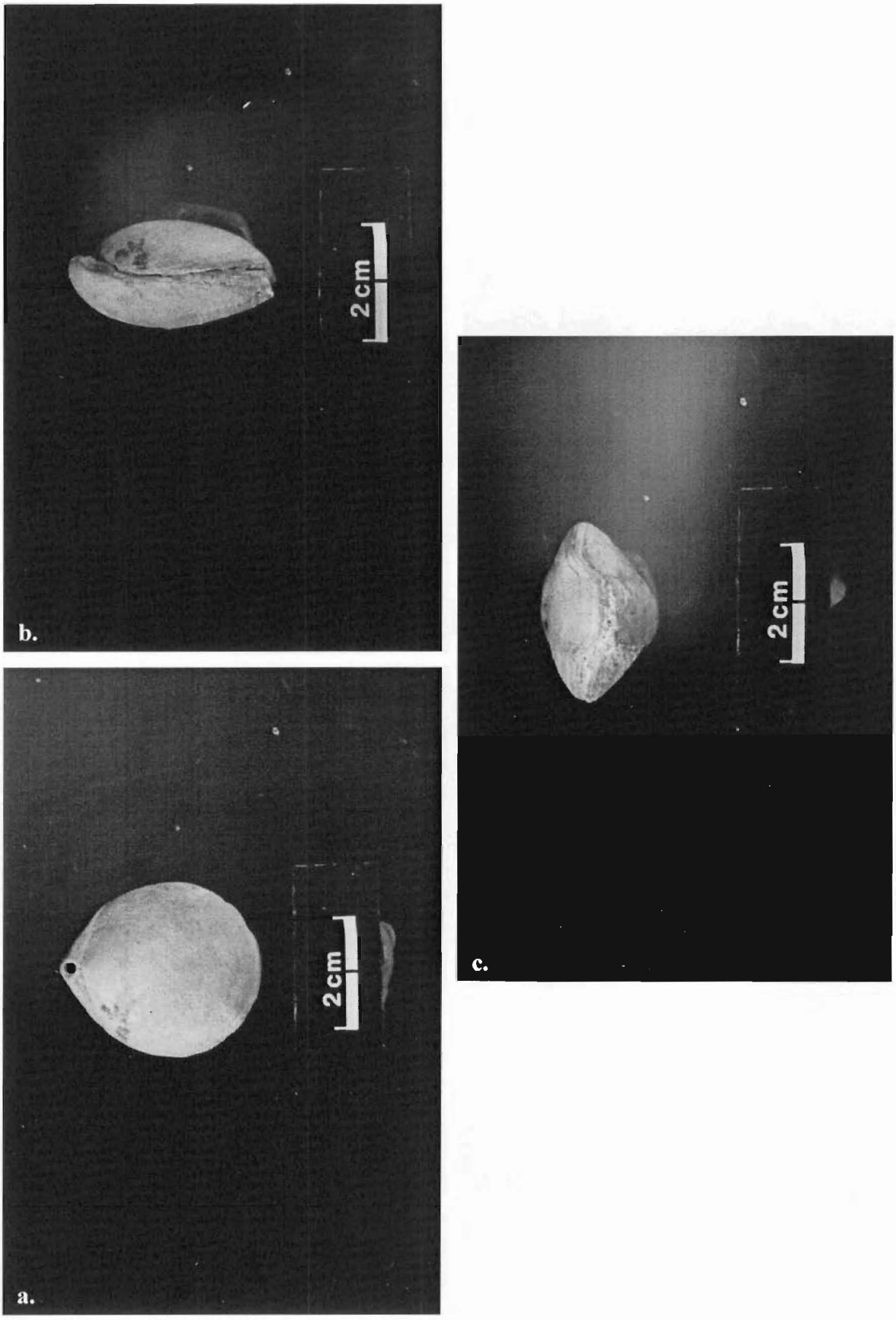


Figure 57. Holotype (Br 127) of *Pachymagas clarkei*.

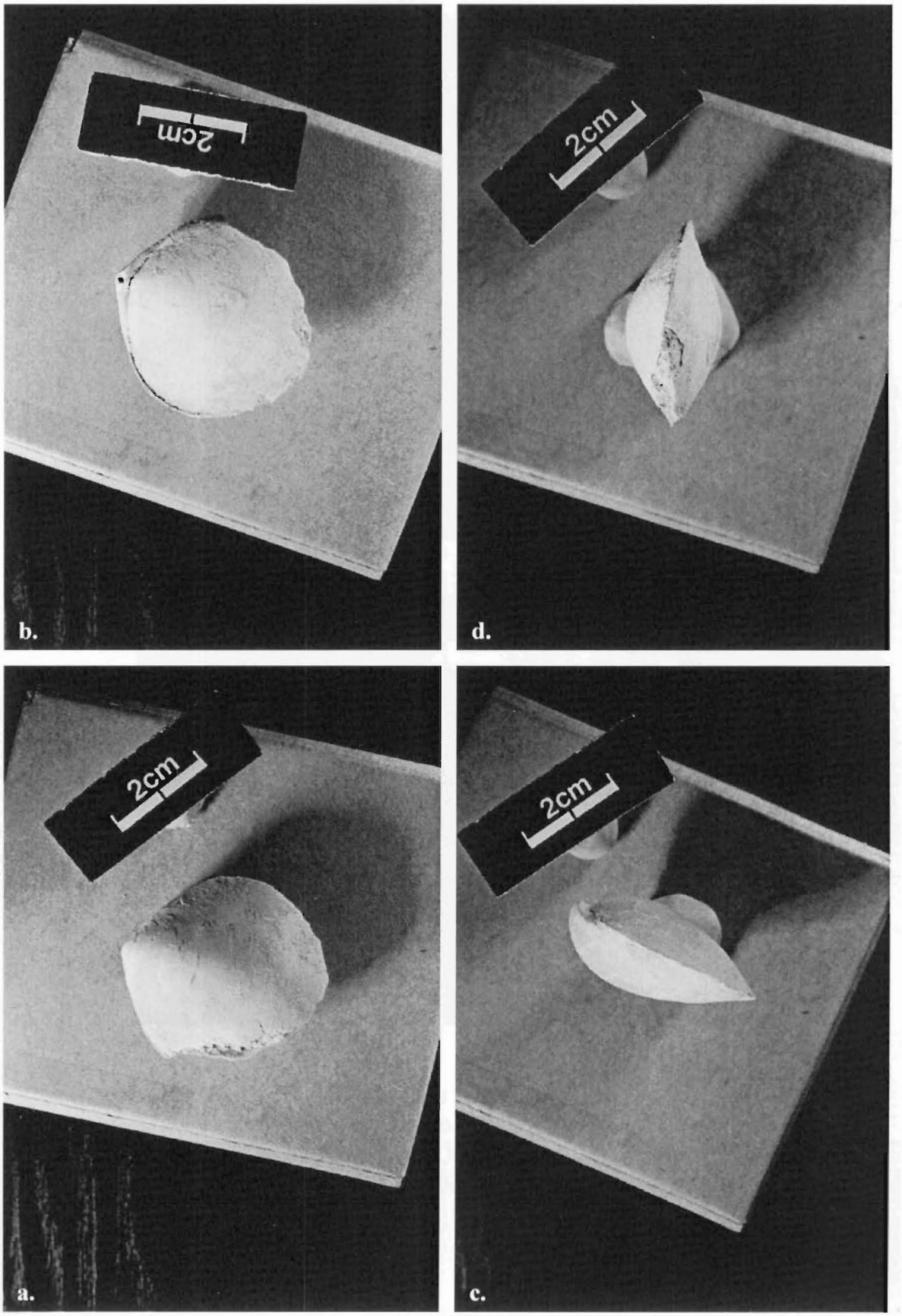


Figure 58. *Waitakia marshalli* (UCM 2017) from Nicholls Road.

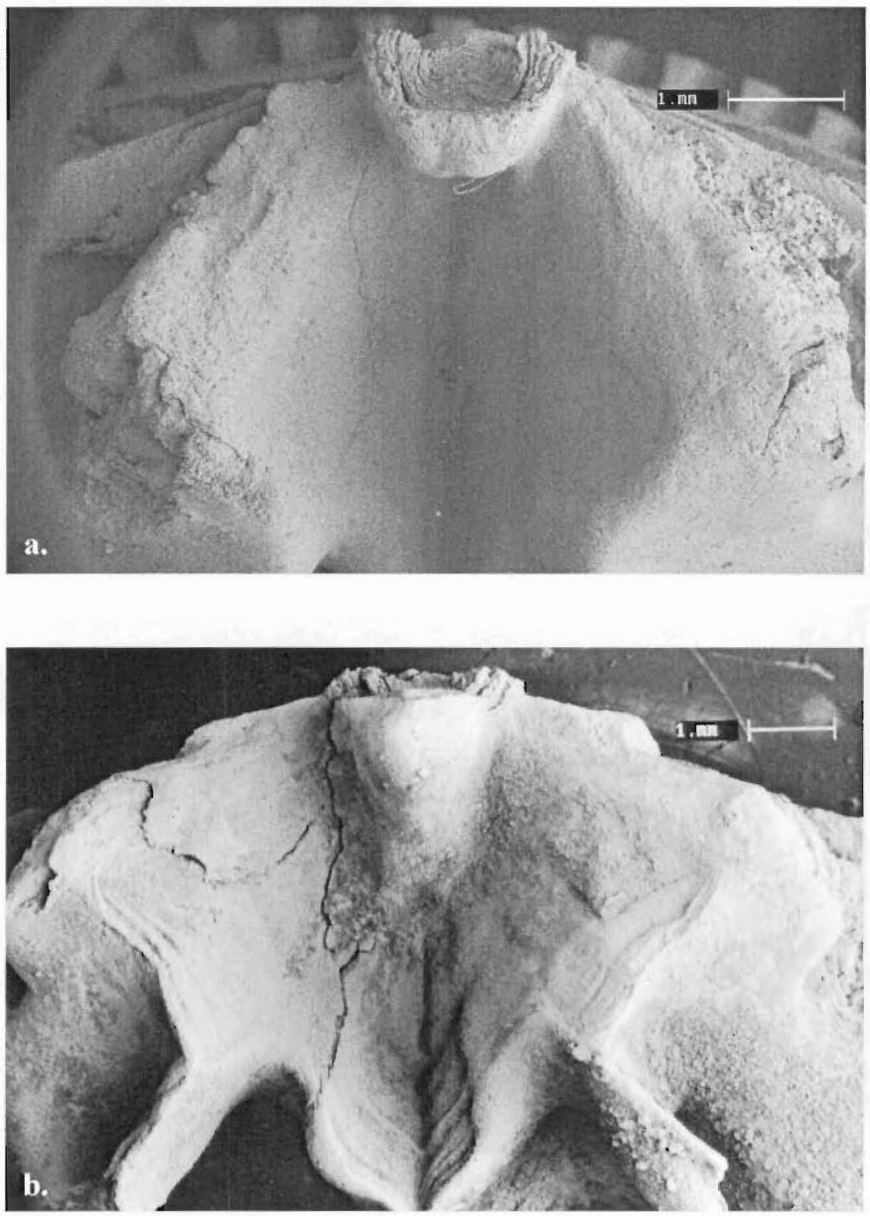


Figure 59. Dorsal interiors of *Waitakia marshalli* from Nicholls Road (**a**: UCM 2022) and Brothers Stream (**b**: UCM 2023). The specimen from Brothers Stream displays a very open hinge-trough with large dorsal pedicle adjustor muscle scars.

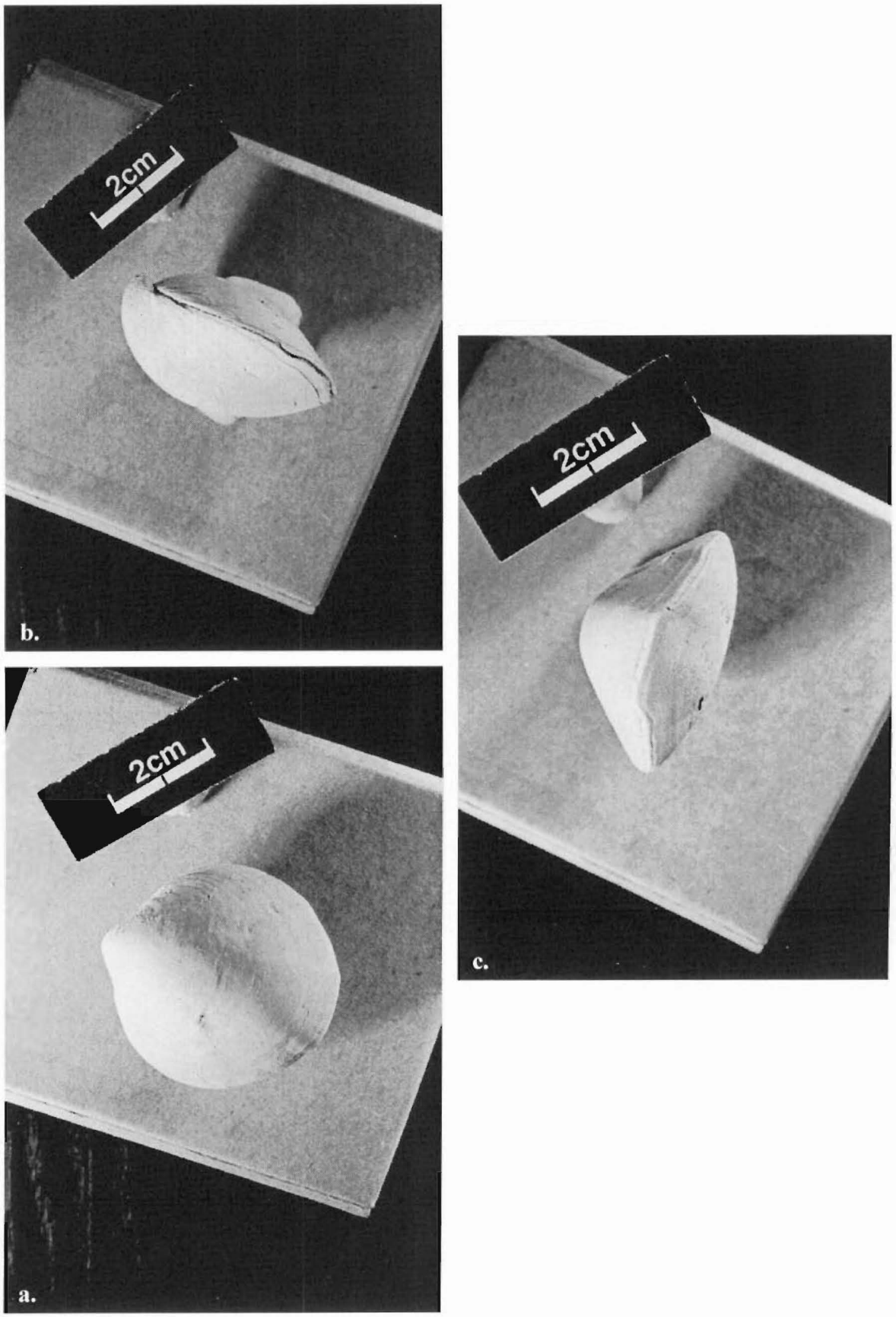
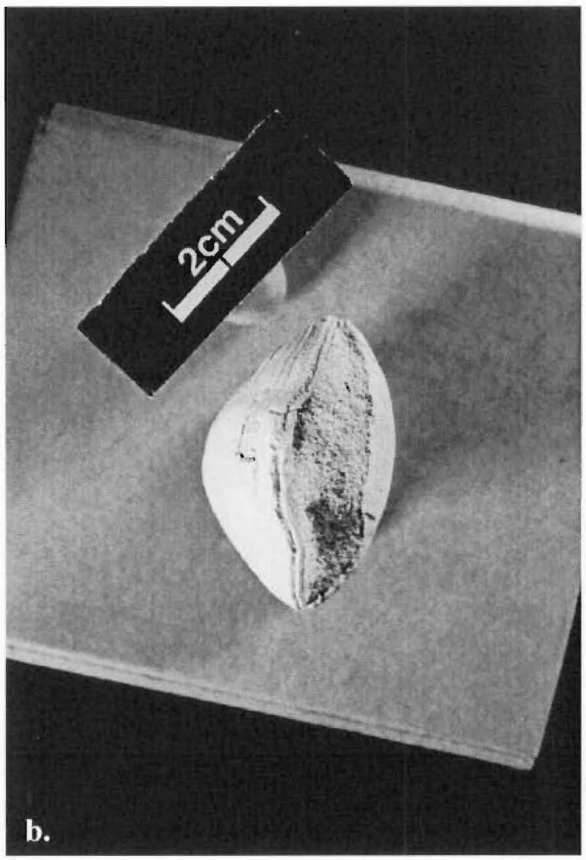
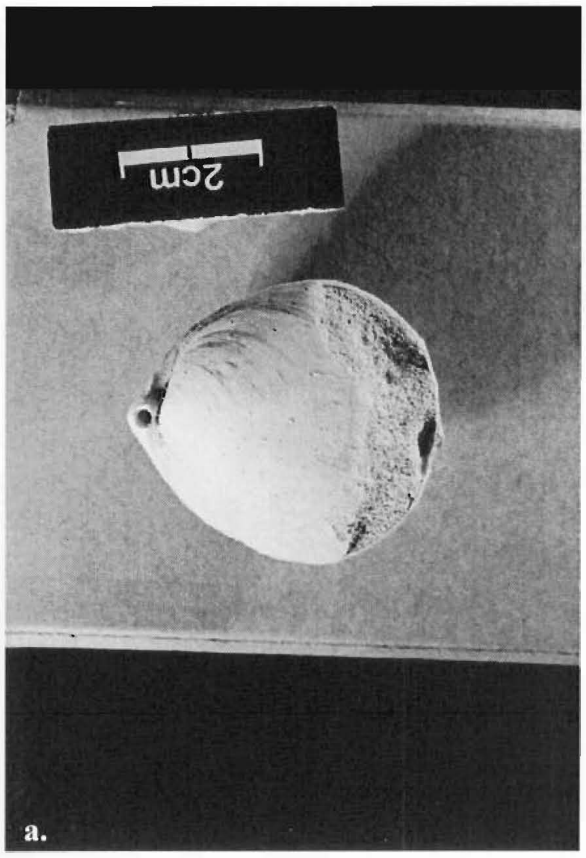


Figure 60. *Waitakia marshalli* (Allan Colln. 27696) from Maerewhenua River.





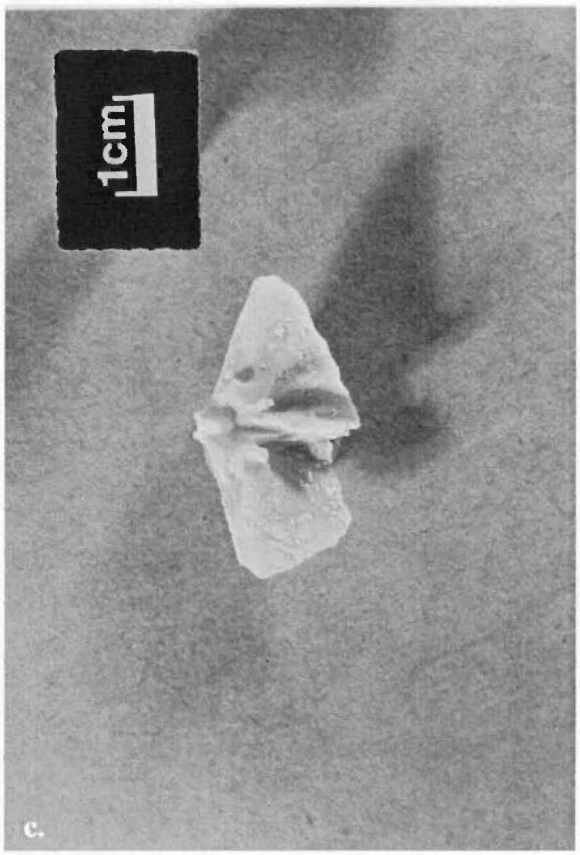


Figure 61. Exteriors (**a**, **b**: UCM 2018) and dorsal interior (**c**: UCM 2019) of *Waitakia marshalli* from Meyers Pass.

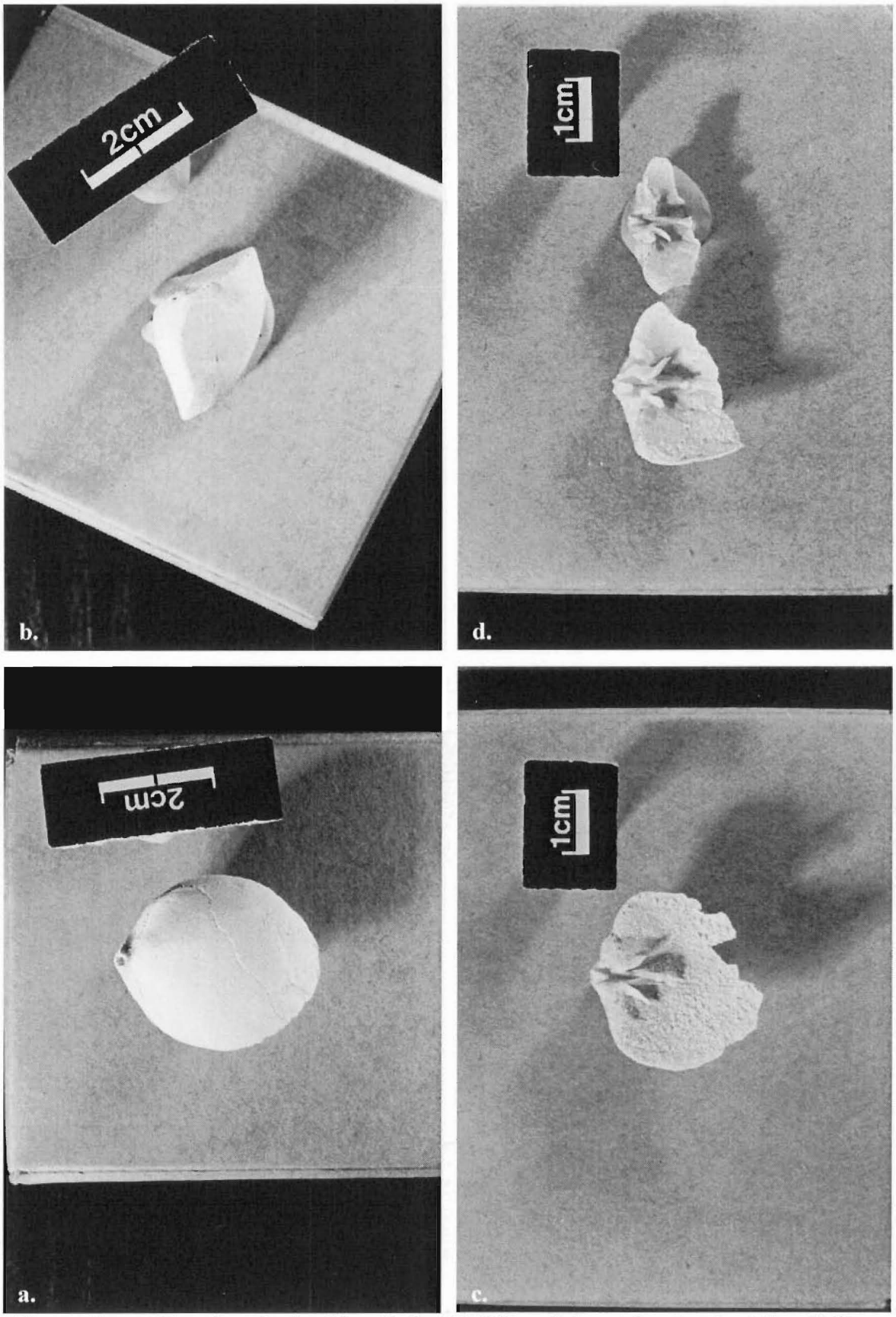


Figure 62. Exteriors (**a**, **b**: Allan Colln. 28632) and dorsal interior (**c**: Allan Colln. 28627) of *Waitakia marshalli* from Onepunga, with further dorsal interiors (**d**: UCM 2020 (large specimen); UCM 2021 (small specimen)) of *W. marshalli* from Whiterock Quarry.

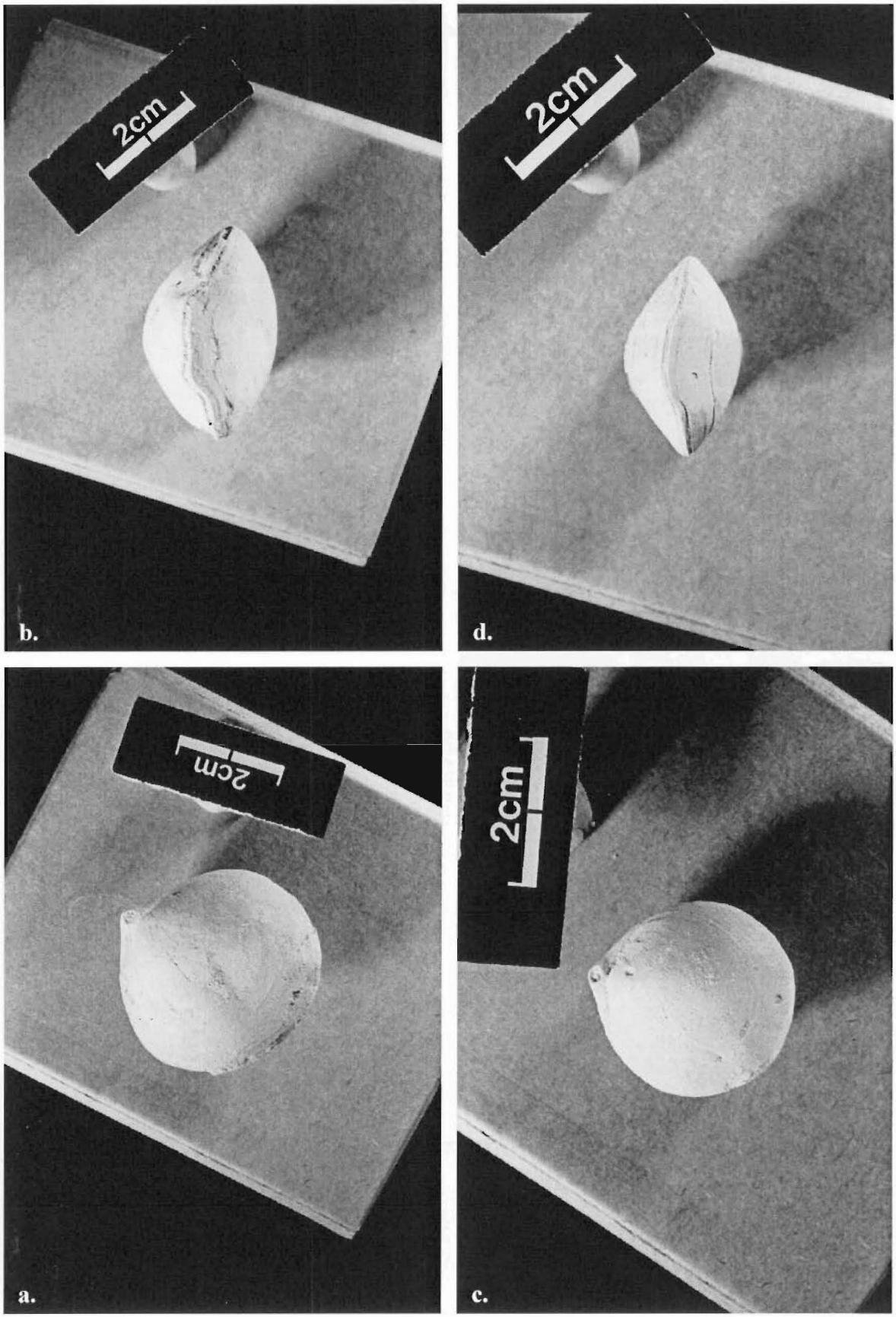


Figure 63. *Waitakia marshalli* (**a**, **b**: Allan Colln. 28057; **c**, **d**: Allan Colln. 28057) from Curiosity Shop.

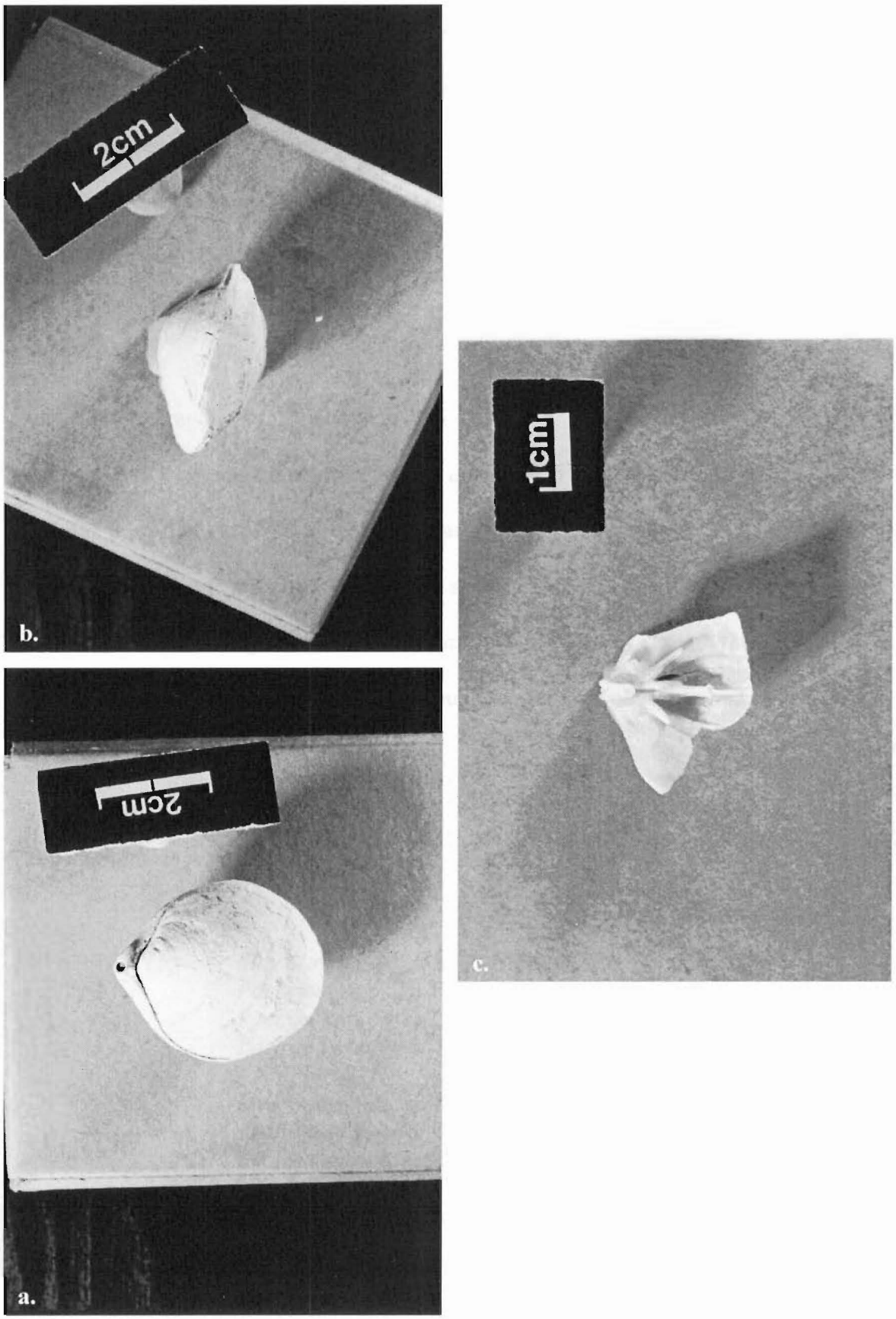


Figure 64. Exteriors (**a**, **b**: Allan Colln. 27989) and dorsal interior (**c**: Allan Colln. 27997) of *Waitakia marshalli* from the South Canterbury Localities Blands Bluff and Fossil Point, respectively.

The description of *Magellania insolita* Hutton 1905 (here synonymised) appears to have been partly based on *Waitakia elliptica* from Duntroon; additional description seems to have been derived from Curiosity Shop material – *Waitakia marshalli* from the Berrydale Greensand exposed at that locality. Hutton's figure (see fig. 46) seems to demonstrate a specimen of *W. marshalli*, doubtless from Curiosity Shop.

From fragmentary material Allan (1940, p. 295) recorded the possible occurrence of *Waiparia elliptica* (*Waitakia elliptica*) in the Balfour Quarry limestone. Material from this locality was examined, and the conclusion drawn that *W. elliptica* does not occur there, rather the descendent species *Waitakia marshalli* is present. The wide hinge-line and large foramen of *W. marshalli* are usually enough to differentiate fragmentary material from *W. elliptica*, though when examining interiors of juveniles it becomes difficult to differentiate the two.

3.10 ***Waitakia parki*** (Hutton, 1905)

SYNONYMY:
Magellania parki Hutton, 1905, p. 276, pl. XLV, fig. 4
Pachymagas parki Thomson, 1915, p. 394-395, fig. 2b
Pachymagas parki Thomson, 1918b, p. 197
Pachymagas parki Thomson 1920, p. 378 and text-fig. 9, pl. XXV, figs 8-11
Pachymagas parki Thomson, 1926, 149-151, 155-156, 158
Pachymagas parki Thomson, 1927, p. 6 text fig. 1
Pachymagas parki Allan, 1937a, p. 121
"*Pachymagas*" *parki* Allan, 1957, p. 106
"*Pachymagas*" *parki* Allan, 1960, p. 243, 264 (stratigraphic range)
Pachymagas parki Levy, 1961, p. 82, 83
"*Pachymagas*" parki Dawson, 1990a, p. 70

TYPE LOCALITY: Oamaru.

Considered by Thomson (1920, p. 378) to have come from "Greensands, Hutchinson's Quarry, Oamaru."

TYPE MATERIAL: Holotype (B1) and paratype (B2) in Canterbury Museum, Christchurch. Hypotypes (Br 125) in the National Museum of New Zealand, Wellington, not located by Keyes (1971).

(Source: Dawson 1990a)

OCCURRENCE: Gee Greensand {North Otago}, at: Hutchinson's Quarry.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (27109-27118, 27125-27130 Hutchinson's Quarry) ; (27131-27164 Hutchinson's Quarry) ; (27298-27359 Hutchinson's Quarry). Unnumbered collections, University of Canterbury: (Hutchinson's Quarry (bag): D. I. MacKinnon Collection).

AGE/RANGE: Altonian

FIGURES: 65-67

DESCRIPTION: Medium to large, smooth, biconvex shell displaying numerous faint growth-lines; shell elliptical; moderately wide cardinal margin gently curved; anterior commissure very strongly narrowly unisulcate. Beak fairly low, obtuse, erect, attrite;

moderately large mesothyrid foramen; beak ridges fairly well defined; gently convex cardinal area with conjunct deltidial plates. Medium septum relatively thickened, extending anteriorly about one-third of valve length, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped hinge-trough with steeply inclined walls; crural bases fused to the thickened inner socket ridges; swelling-together of the crural bases confines the dorsal pedicle adjustor muscle attachment sites to the posterior of the hinge-trough. Cardinal process consisting of roughened myophore with boss-like anterior swelling that projects ventrally occupies posterior one-third of the hinge-trough, often tapering anteriorly to occupy up to one-half of the hinge-trough; wing-like projections of myophore develop posteriorly. Dorsal adductor muscle scars are large and distinct, terminating anteriorly at approximately the termination point of the median septum – at one-third the length of the valve. The large muscle-field scars of the ventral valve are impressed such as to produce a low median ridge in the valve floor between the scars. The teeth are large and sturdy, and are perched on swollen bases, which are grooved to accommodate the swollen inner socket ridges. Adult loop trabecular, the transverse connecting band very attenuated.

DISCUSSION: Thomson (1926) considered the *Pachymagas* greensands of the Oamaru coastal district to be "Hutchinsonian" in age, but noted that the fauna at Hutchinson's Quarry differed in character from that at other localities (Landon Creek, Deborah, Rifle Butts, Devil's Bridge) – *P. haasti* and *P. hectori*, while common at these localities, was said to be rare at Hutchinson's Quarry, though *P. parki* occurred in abundance. Thomson also noted that *Rhizothyris* was rare elsewhere other than Hutchinson's Quarry, where it was very common. Considering the strongly folded nature of the shell and relatively large cardinal process advanced features (as

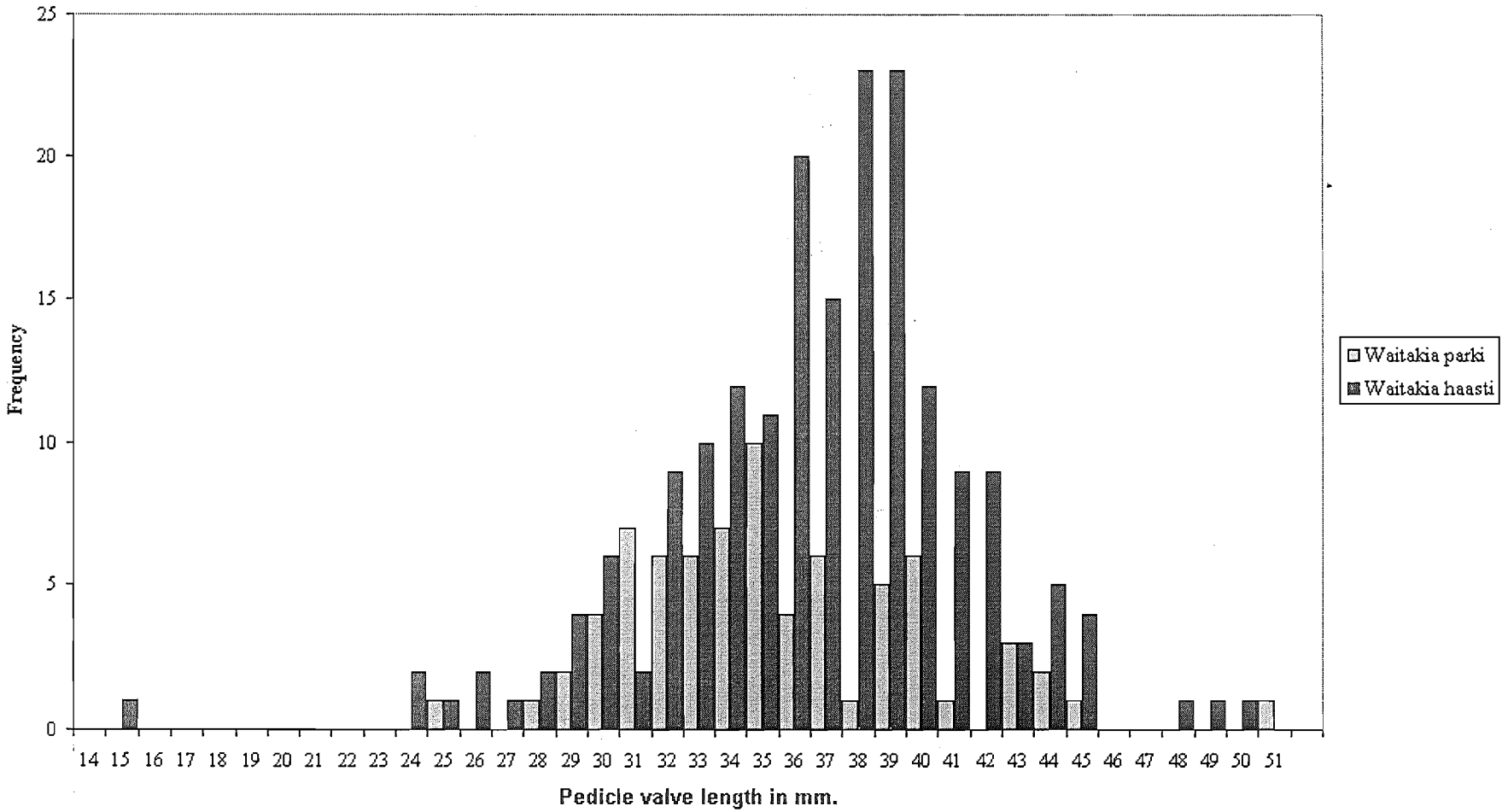
compared with the "little advanced cardinal processes or folding" of *haasti-hectori*), Thomson speculated that the Hutchinson's Quarry fauna might exist at a different, younger horizon than the fauna found at the other localities. Finlay (1939a) and Finlay & Marwick (1940) introduced the term "Lower Hutchinsonian" based on the "less advanced" brachiopods of Landon Creek etc. interpreted to represent an older horizon. The "Lower Hutchinsonian" was later given separate stage (Otaian) status by Finlay & Marwick (1947), while the "True Hutchinsonian" was split into the Altonian and Clifdenian stages by Scott (1972). See section 1.5 for detailed discussion of New Zealand stage names relevant to this study.

The commissure of *W. parki* is characteristically very strongly unisulcate (fig. 66d); Thomson (e.g. 1920, 1926) considered presence of folding an advanced feature, but it was found in this study that, at least for *Waitakia*, the degree of folding present in a shell seems to be largely independent of the presence of an advanced cardinal process within the shell. The 'interior' and 'exterior' growth fields are considered to be dissociated, or at least the degree of correlation between the two is not (very) high.

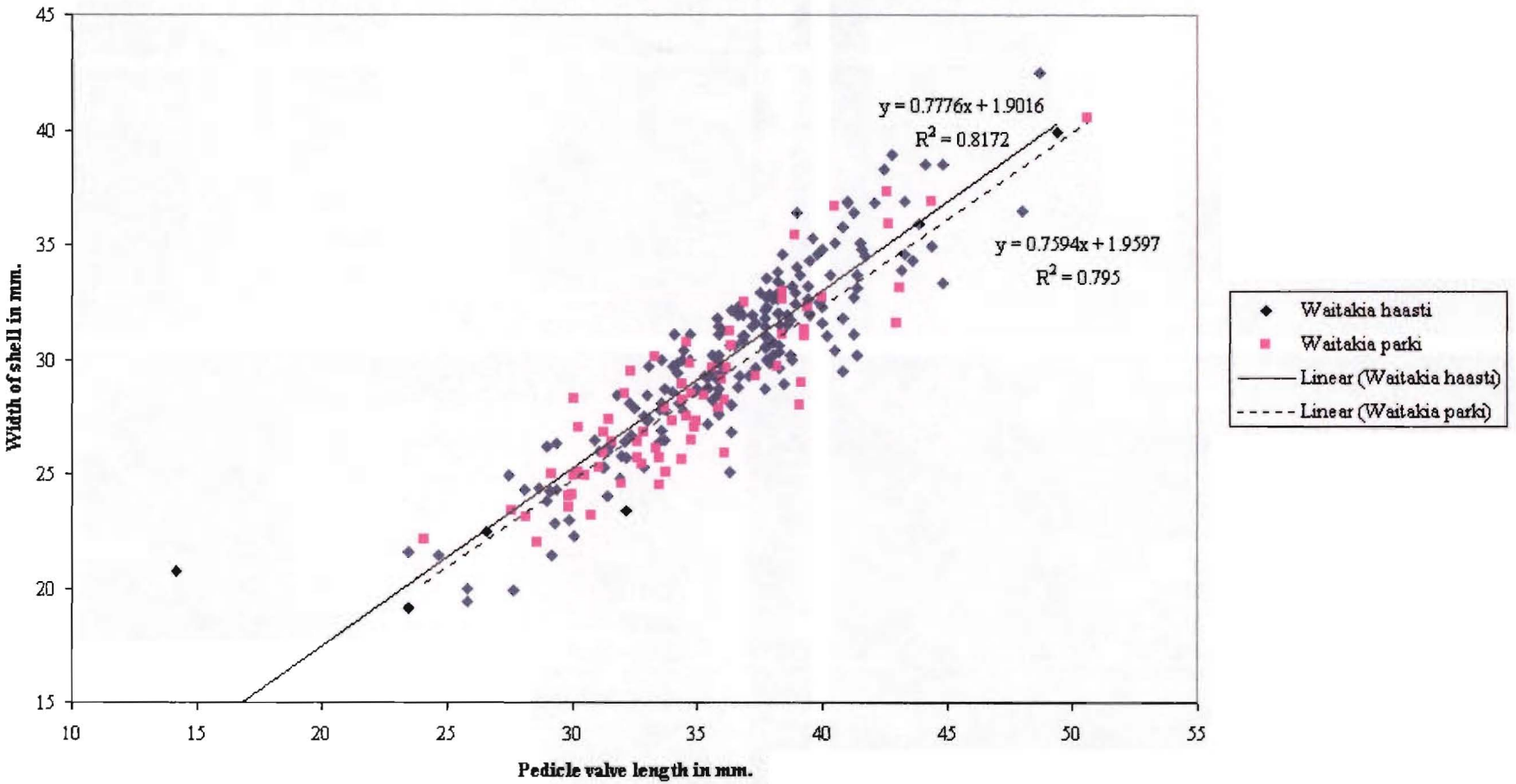
As has already been stated in the discussion for *Waitakia haasti*, the current re-investigation reveals that the cardinalia of *Waitakia parki* is not of a *more advanced* aspect than that of *W. haasti* (as in Thomson's (1920) view), but is rather *consistently* moderately advanced, where *W. haasti* has a lower incidence of possession of an advanced process. Figure 67 demonstrates the cardinal characteristics of a typical specimen of *W. parki*.

The mean lengths of measured specimens of *Waitakia parki* and *W. haasti* differ, being 34.9 mm. and 36.3 mm. respectively. The unimodal histograms of

Graph 17: Histogram of pedicle valve length for Waitakia parki and Waitakia haasti



Graph 18: Pedicle valve length vs. Width of shell for Waitakia haasti and Waitakia parki (one outlier has been removed)



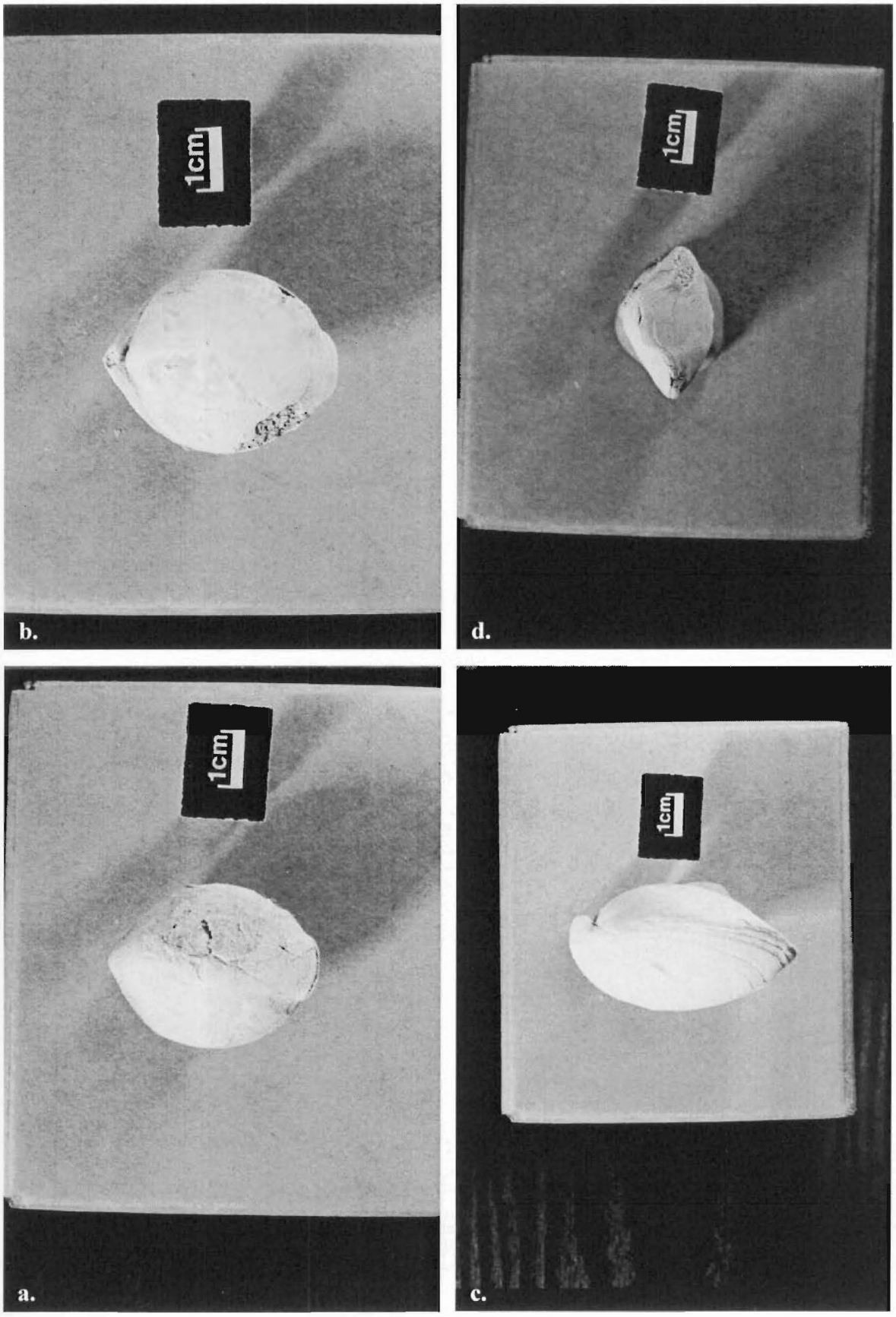


Figure 65. Holotype (B1) of *Pachymagas parki*.

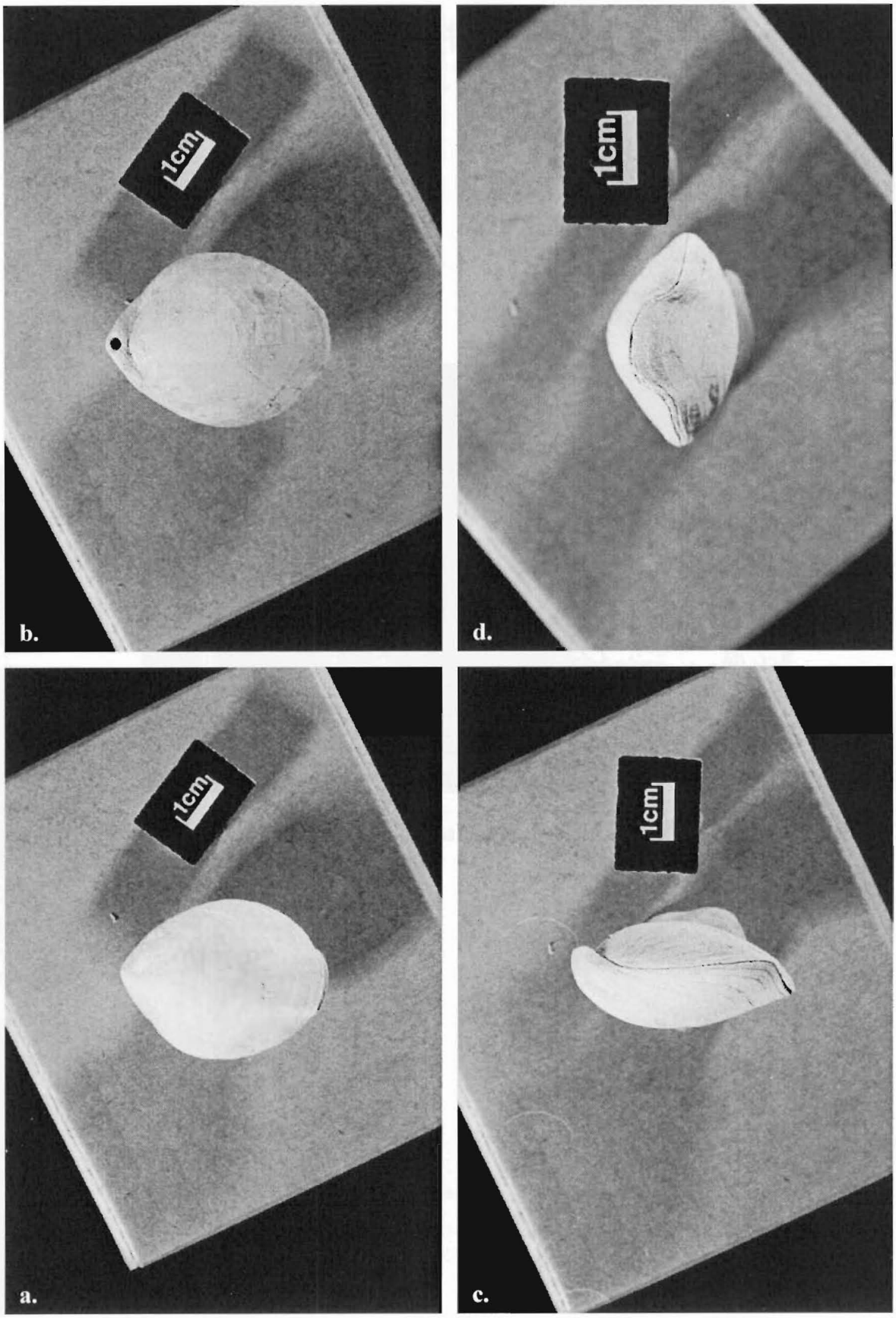


Figure 66. *Waitakia parki* (Allan Colln. 27111) from Hutchinson's Quarry.

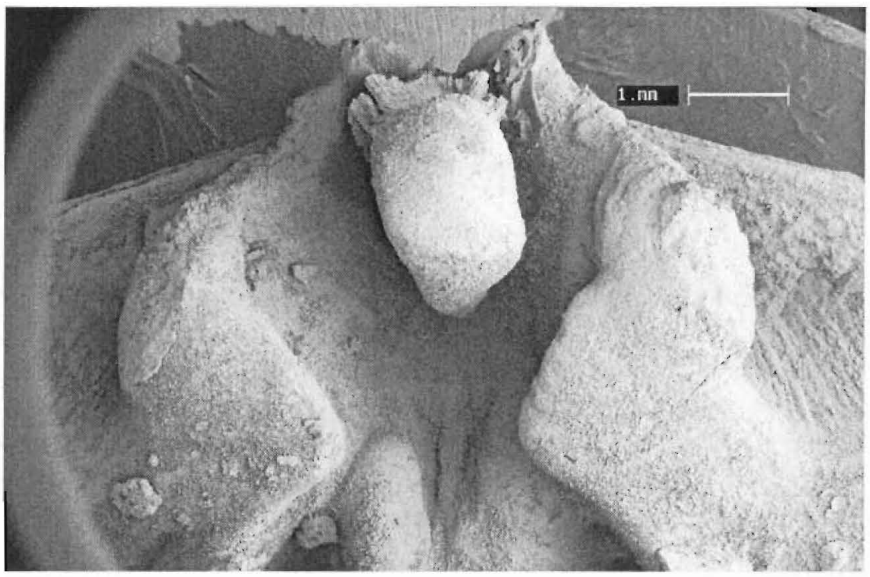


Figure 67. Dorsal interior of *Waitakia parki* (UCM 2005) from Hutchinson's Quarry.

pedicle valve length for *parki* and *haasti* indicate that population structures were significantly different, though the growth trajectory for length and width (as demonstrated by similarity in slope and position of the regression line in a scatter plot) does not appear to differ significantly – graphs 17 and 18, respectively. It is moderately surprising that the growth trajectory for length and width does not differ, as the shell of *parki* is extremely unisulcate, and it might be expected that this would perturb growth trajectories somewhat. However, it seems that production of the sulcus in the growing shell did not effect other growth trajectories, suggesting a high level of independence between the various shell growth trajectories.

Waitakia parki is retained as a valid species (rather than being synonymised with *W. haasti*) because of its observed consistently moderately advanced cardinal process, and its characteristic very strong sulcation. It could be argued that the differences, especially the sulcation, are merely ecophenotypic, and that *parki* is just a younger representative of *haasti*. This is a possibility, though the exteriorly similar *Rhizothyris amygdala* (Bowen & Campbell 1973) which also occurs in abundance at Hutchinson's Quarry does not demonstrate great unisulcation, as might be expected if characteristics of the environment were responsible for the production of the strong sulcation seen in *W. parki* – i.e. an analogous response in *R. amygdala* might be expected.

3.11 *Waitakia* (?) *trelissickensis* (Thomson, 1918)

SYNONYMY: *Pachymagas trelissickensis* Thomson, 1918a, p. 118
"*Pachymagas*" *trelissickensis* Allan, 1960, p. 239, 264 (stratigraphic range)
"*Pachymagas*" *trelissickensis* Dawson, 1990a, p. 71

TYPE LOCALITY: New Zealand Geological Survey Macropalaeontology Collection locality 449: "lower beds, Trelissick Basin, Canterbury, Enys, 1880".

TYPE MATERIAL: Holotype (Br 1271) in the National Museum of New Zealand, Wellington.

(Source: Dawson 1990a)

OCCURRENCE: Marine basaltic tuffs of the Thomas Formation, Broken River, mid-Canterbury.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (28243-28246 White Water Creek) ; (28247-28257, 28272-28277, 28295, 28296 Castle Hill). Unnumbered collections, University of Canterbury: (Junction of Porter and Thomas Rivers (2 bags): S. Fryer MSc. Thesis Collection).

AGE/RANGE: Duntroonian or Waitakian

FIGURES: 68, 69

DESCRIPTION: Medium to large, smooth, biconvex shell displaying numerous faint growth-lines; shell elongately oval or sub-pentagonal in outline; wide cardinal margin gently curved; anterior commissure incipiently to weakly unisulcate. Beak produced, obtuse, suberect, attrite; very large circular foramen; beak ridges well defined; gently convex cardinal area with conjunct deltidial plates; prominent ventral palintrope. Median septum slender, extending anteriorly about one-half valve length, bifurcating

posteriorly to unite with the hinge-plates, forming a v-shaped hinge-trough with shallowly to steeply inclined walls; crural bases fused to the thickened inner socket ridges. Cardinal process consisting of roughened myophore with boss-like anterior swelling occupies one-half of the hinge-trough; wing-like projections of myophore develop posteriorly. Dorsal adductor muscle scars are large and distinct, terminating anteriorly at approximately the termination point of the median septum – at one-half the length of the valve. The teeth are large and sturdy, and are perched on swollen bases. Adult loop trabecular.

DISCUSSION: Allan Colln. Specimens 28254 and 28255, from Castle Hill, appear to be *W. trelissickensis*, but are very large – measuring approx. 52 and 50 mm. in length, respectively. The two specimens are covered in matrix but are fragile, so no attempt to clean them was made. The remaining material ascribed to *trelissickensis* is on average approx. 35 mm. in length. Exteriorly *W. trelissickensis* somewhat resembles *Neothyris* (?) *anceps* Thomson, specimens 28254 and 28255 being of a similar size (though *anceps* itself does demonstrate a significant range in size) to typical *anceps* from the Glenmark Limestone Member of the Mount Brown Formation at Weka Pass. It is a possibility that the two species are related, and that *W. trelissickensis* is an ancestral form, or an early representative, of *Neothyris* (?) *anceps*. This possibility was not examined further in this study.

The tuffaceous strata from which this species comes is either Duntroonian or Waitakian in age (Gage, 1970). Allan (1960) stated that foraminal evidence suggested a Duntroonian age, but gave no source for this evidence. All microfossil samples taken from the Thomas Formation for Gage's study were determined as Duntroonian (Gage 1970, p. 525). *Waitakia trelissickensis* is tentatively considered in this study to

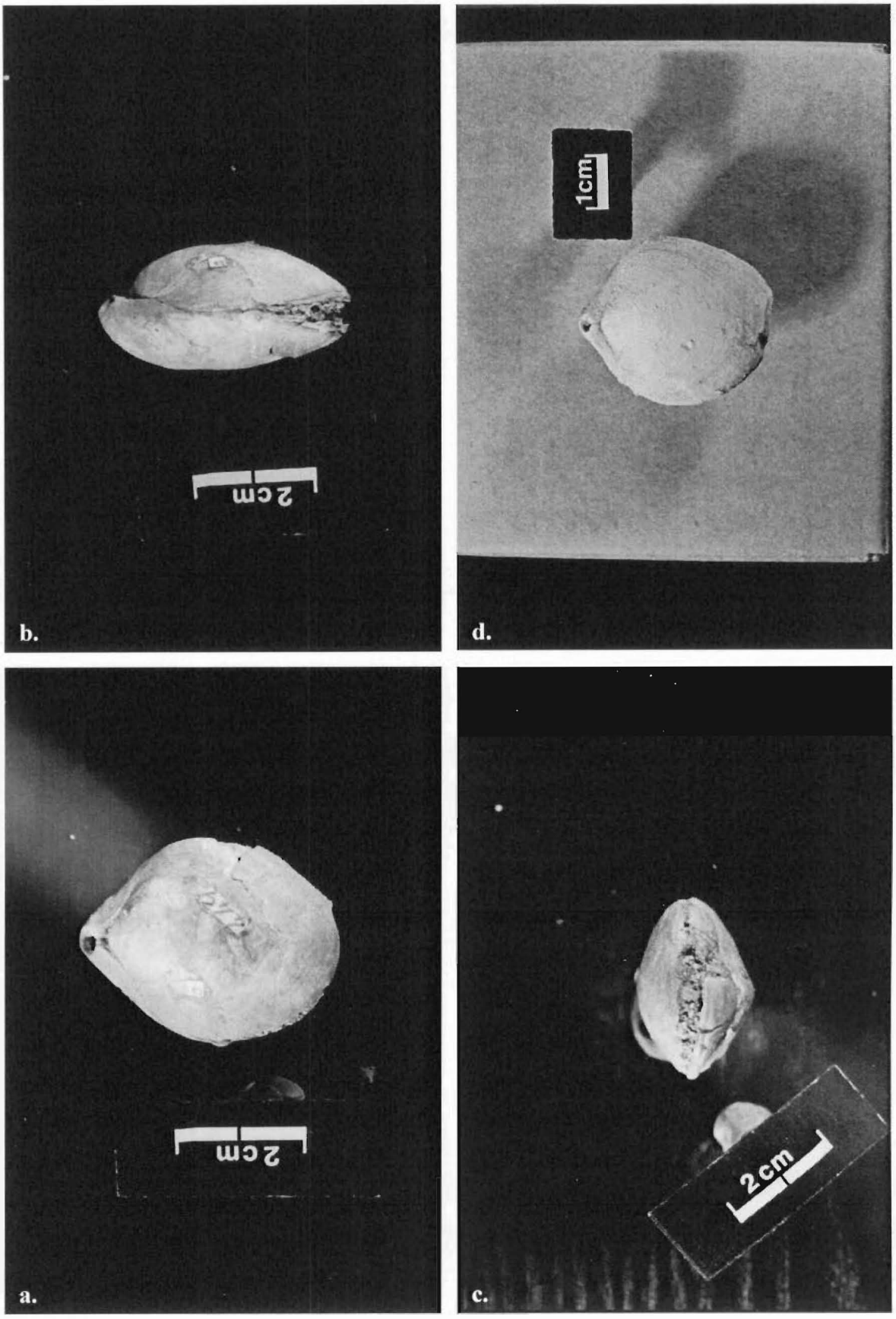


Figure 68. Holotype of *Pachymagas trelissickensis* (**a**, **b**, **c**: Br 1271) and dorsal exterior of *Waitakia* (?) *trelissickensis* (**d**: Allan Colln. 28244; White Water Creek, mid-Canterbury).

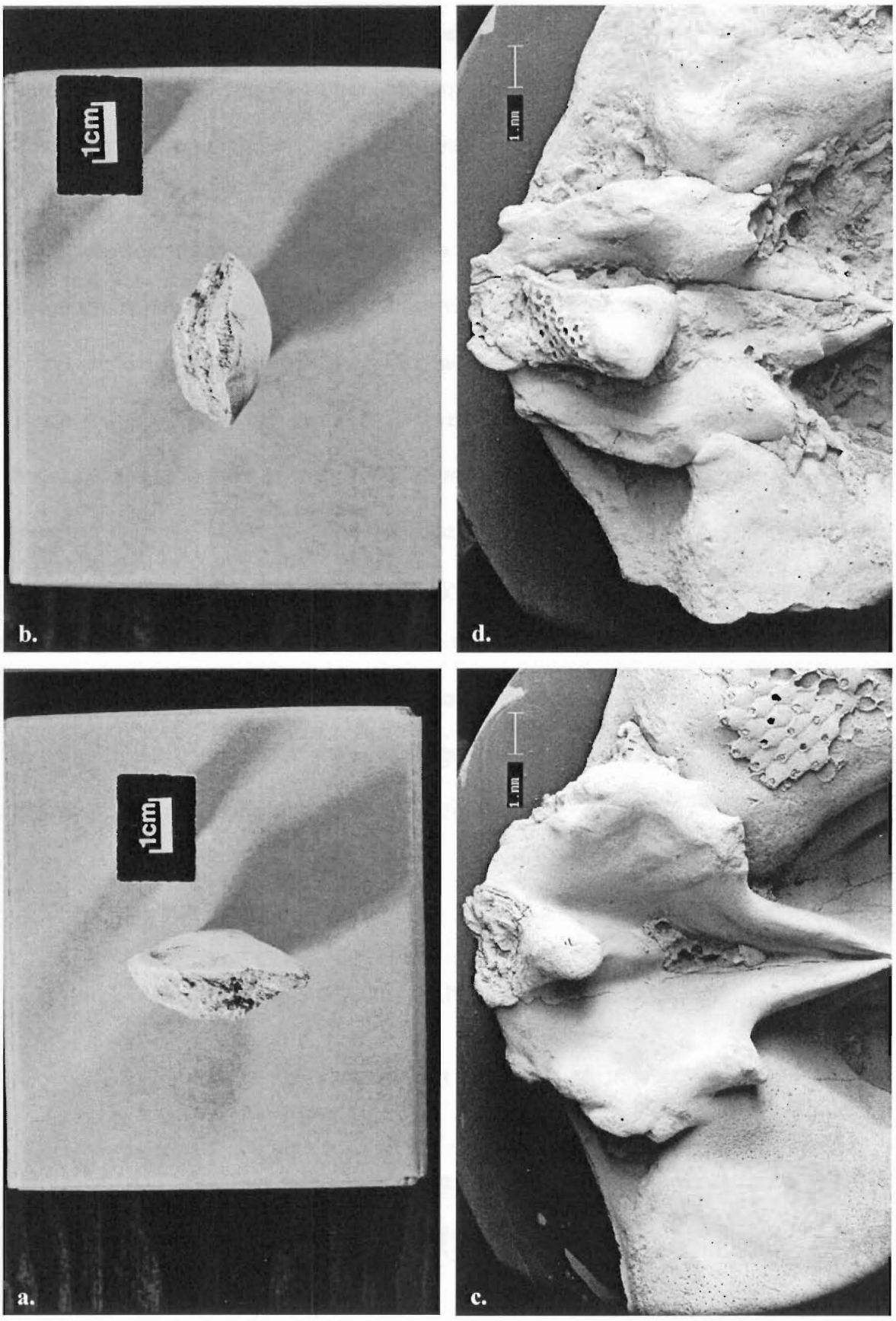


Figure 69. Exteriors (**a**, **b**: Allan Colln. 28244) and dorsal interiors (**c**, **d**: both specimens Allan Colln. 28246) of *Waitakia* (?) *trelissickensis* from White Water Creek, mid-Canterbury.

have evolved from *Waitakia elliptica* (see section 4.0), the Duntroonian form, but this opinion does not favour a Duntroonian over a Waitakian age for *trelissickensis*. Therefore the age of this fossil must be listed as Duntroonian or Waitakian.

Examination and description of this species is made difficult through lack of specimens, and poor preservation. These two factors go hand in hand as the poor preservation leads to few successful extractions from the rock face; few of these fossils extracted survive cleaning or excavation intact. This is due to the diagenetic history of the tuffaceous beds in which *W. trelissickensis* is found. The aragonitic and most of the calcitic fauna of the marine tuffs has been dissolved, the calcium carbonate precipitated throughout the rock, especially in fractures and the insides of surviving brachiopod shells. The material that has survived this process is hard to extract, and once extracted, the calcite has to be successfully removed from the interiors of the fragile shells – a difficult process. Figure 69d demonstrates some of the calcite retained in the hinge-trough after excavation.

Subfamily **MAGELLANINAE** Beecher, 1895

Genus ***Pycnozygus*** Hiller & MacKinnon in prep.

ETYMOLOGY: From the Greek *pyknos* (= thick) and *zygos* (= yoke) alluding to the thickened cardinalia and robust brachidia of the genus.

TYPE SPECIES: *Pachymagas balfourensis* Allan, 1940

STRATIGRAPHIC RANGE: Waitakian-Altonian (Early Miocene-Middle Miocene); New Zealand.

DIAGNOSIS: Large, smooth, strongly biconvex shells, broadly subpentagonal to broadly ovate in outline; anterior commissure weakly to moderately strongly very broadly unisulcate. Beak erect to incurved, attrite, circular foramen fairly small, mesothyrid. Beak ridges well defined; cardinal area gently convex, with broad symphytium. Cardinal process incorporates an anterior rounded lobe and lateral rim extending posteriorly, together forming a cup-shaped platform in the centre of which the diductor muscles attached. Shell interior demonstrates extensive secondary shell thickening of the posterior; inner socket ridges and crural bases almost fused medially with the rounded lobe of the cardinal process. Median septum thickened, bifurcating posteriorly to unite with the hinge-plates, and extending anteriorly approximately one-third to one-half of dorsal valve length. Adult loop teloform.

DISCUSSION: The species placed in *Pycnozygus* were originally placed in "*Pachymagas*" – *Waitakia* of this study. This was due to original establishment of the species without knowledge of interior characteristics, the species here considered to differ at subfamily level based on such characteristics. The genus is interpreted to have been free-lying on soft substrates, the beak commonly incurved, the foramen small, both suggesting the pedicle was not active. The thickening of the posterior of the valves would have helped weight the shell, keeping it in place on the substrate, the shape probably helping to distribute the weight of the shell evenly, preventing the shell from sinking into soft substrates.

3.12 *Pycnozygus triangularis* (Hutton, 1873)

SYNONYMY:

Waldheimia triangulare Hutton, 1873, p. 36
Magellania triangularis Hutton, 1905, p. 477
Pachymagas triangularis Thomson, 1927, p. 287
Pachymagas balfourensis Allan, 1940, p. 294-295, pl. XXXVII, figs. 1-3
"*Pachymagas*" *balfourensis* Allan, 1960, p. 240, 263 (stratigraphic range)
"*Pachymagas*" *triangularis* Allan, 1960, p. 252, 264 (stratigraphic range)
Pachymagas balfourensis Levy, 1961, p. 86
Pachymagas triangularis Keyes, 1971, p. 82
"*Pachymagas*" *balfourensis* Dawson, 1990a, p. 62
"*Pachymagas*" *triangularis* Dawson, 1990a, p. 71

TYPE LOCALITY: Oamaru, North Otago.

Keyes (1971, p. 82) stated that, from examination of matrix adhering to the type, N. de B. Hornibrook had determined the holotype had come from the Gee or Kokoamu Greensand. It is considered here that the type locality might have been incorrectly recorded, as no further material has been found from either of these greensands, and an identical species is found in the Balfour Quarry limestone, being previously recorded as *Pachymagas balfourensis* by Allan (1940).

TYPE MATERIAL: Holotype (Br 118) in the National Museum of New Zealand, Wellington. Holotype (UCM 1473) and paratypes (UCM 1474 a-j) of *Pachymagas balfourensis* Allan 1940 in the Department of Geological Sciences, University of Canterbury, Christchurch. Topotype (B210) of *Pachymagas balfourensis* Allan 1940 in Canterbury Museum, Christchurch.

(Source: Dawson 1990a)

OCCURRENCE: "Balfour Lime Company's quarry, south of Balfour township, and N.E. of the long fault scarp of the Hokonui Hills, New Zealand." (Allan 1940, p. 295)

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (26000-26124 Balfour Quarry).

AGE/RANGE: Waitakian

FIGURES: 70-74

DESCRIPTION: Medium to large, smooth, ventribiconvex shell displaying numerous faint growth-lines; shell broadly subpentagonal, with inflated ventral valve strongly carinated posteriorly; wide cardinal margin almost straight; anterior commissure strongly very broadly unisulcate. Beak obtuse, attrite, erect to incurved; fairly small circular mesothyrid foramen; beak ridges well defined; gently convex cardinal area with broad symphytium, developing from conjunct deltidial plates in juveniles. Median septum thickened, extending anteriorly about one-half of valve length, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped hinge-trough with shallowly inclined walls; crural bases fused to thickened inner socket ridges. Gross thickening and infilling of the hinge-trough in the adult obscures/obliterates evidence of juvenile developmental phases for the cardinalia, the above relationships established through examination of juvenile dorsal interiors. Cardinal process consisting of roughened myophore is small and pyramidal in juveniles, with an anterior boss-like swelling extending to occupy one-half of the hinge-trough; with growth the cardinal process develops to consist of an anterior rounded lobe and lateral rim, together forming a cup-shaped platform in the centre of which the diductor

muscles attached. In the most developed specimens, the lateral rims are folded up overtop of the cup-shaped depression, forming a narrow tube into which the diductor muscles extend; the crural bases and inner socket ridges are in the process of fusing medially with the large rounded anterior swelling of the cardinal process, the pedicle adjustor muscles being confined to two small pits either side of the rounded lobe. Dorsal adductor muscle scars are large and terminate anteriorly at approximately the termination point of the median septum – at one-half the length of the valve. The teeth are large and sturdy, and rest upon relatively swollen bases, which are shallowly grooved to partially accommodate the swollen inner socket ridges. Adult loop teloform.

DISCUSSION: As indicated above, it is considered here that *Pachymagas triangularis* is the senior synonym, the type probably having come from Balfour Quarry or thereabouts despite both Hutton's (1873) record of it from Oamaru and Hornibrook's (Keyes 1971, p. 82) determination that the type had been taken from either the Gee or Kokoamu Greensand. The possibility that the holotype did come from either of these greensands shouldn't be disregarded altogether, as the closely related (ancestral?) species *Pycnozygus turneri* appears to occur in the Gee Greensand in very small numbers (one specimen – Allan Colln. 26949, University of Canterbury), and its occurrence there is very easily overlooked; occurrence of *P. triangularis* in the Greensands of North Otago may have been similarly overlooked. Also of consideration is the occurrence of *Waitakia marshalli* in large numbers in North Otago, though it is found in the Otekaike Limestone, and not in the Greensands. Exteriorly some specimens of *W. marshalli* can resemble *P. triangularis* significantly, and there may have been some misidentifications by past authors along these lines.

Conceivably Hutton might have recalled the prominent occurrence of the exteriorly similar *W. marshalli* of the Waitaki Valley, and mislabelled his holotype as coming from the area.

As to the similarity in external form of *W. marshalli* and *P. triangularis*, the two specimens are seen to occur together at Balfour Quarry, perhaps suggesting common adaptations to a common environment. From examination of fragmentary material Allan (1940) suggested that *Waiparia elliptica* (*Waitakia elliptica*) might also be present. It is in fact *Waitakia marshalli* that is present, distinguished from *elliptica* by its relatively broader hinge-line and significantly larger foramen, along with the discriminatory characteristics of the cardinalia in dorsal interiors of adult specimens (section 3.9). The occurrence of *W. marshalli* with *P. triangularis* at Balfour Quarry might make one cautious of ruling out the possibility of *P. triangularis* occurring with *W. marshalli* in the Waitaki Valley, and with it the possibility that the holotype does come from North Otago rather than Southland.

Allan (1940) suggested comparison with the South American species *Pachymagas venter* (von Ihering), noting that *P. balfourensis* (*P. triangularis*) resembles *P. venter* in the pronounced carination and early sulcation of the ventral valve, and in the incurvature of the beak. Thomson (1927) listed *triangularis* under species of the *Pachymagas venter* series, and Allan voiced agreement with Thomson's view that the *Pachymagas venter* series (Thomson 1927), and hence *triangularis* along with it, might be generically distinct. Hiller & MacKinnon in prep. note that *Pachymagas venter* (von Ihering) has a trabecular loop, conjunct deltidial plates, and cardinalia that differs from that of *P. balfourensis* (*P. triangularis*). They place *P. balfourensis* in the new genus *Pycnozygus*.

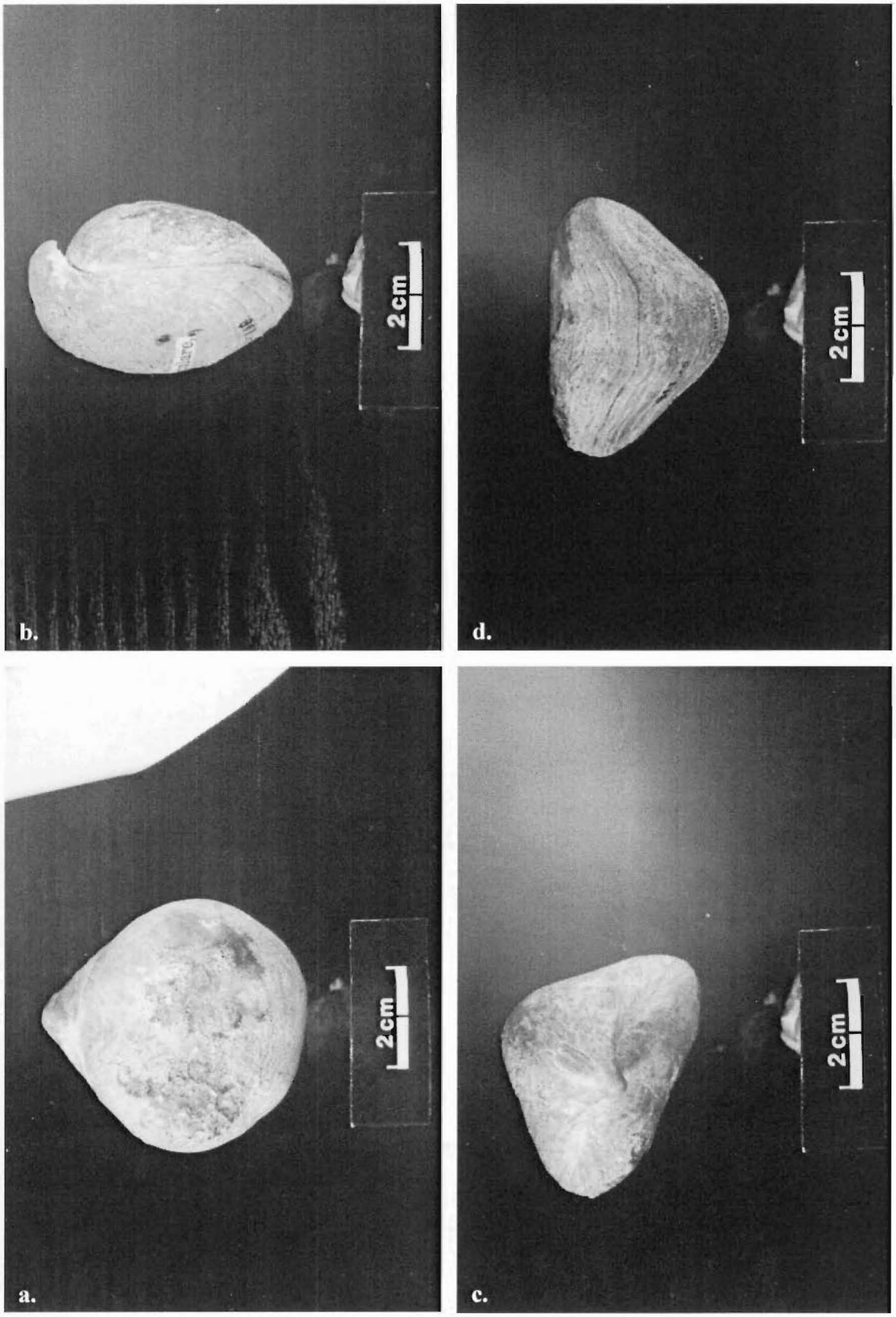


Figure 70. Holotype of *Pachymagas triangularis* (Br118).

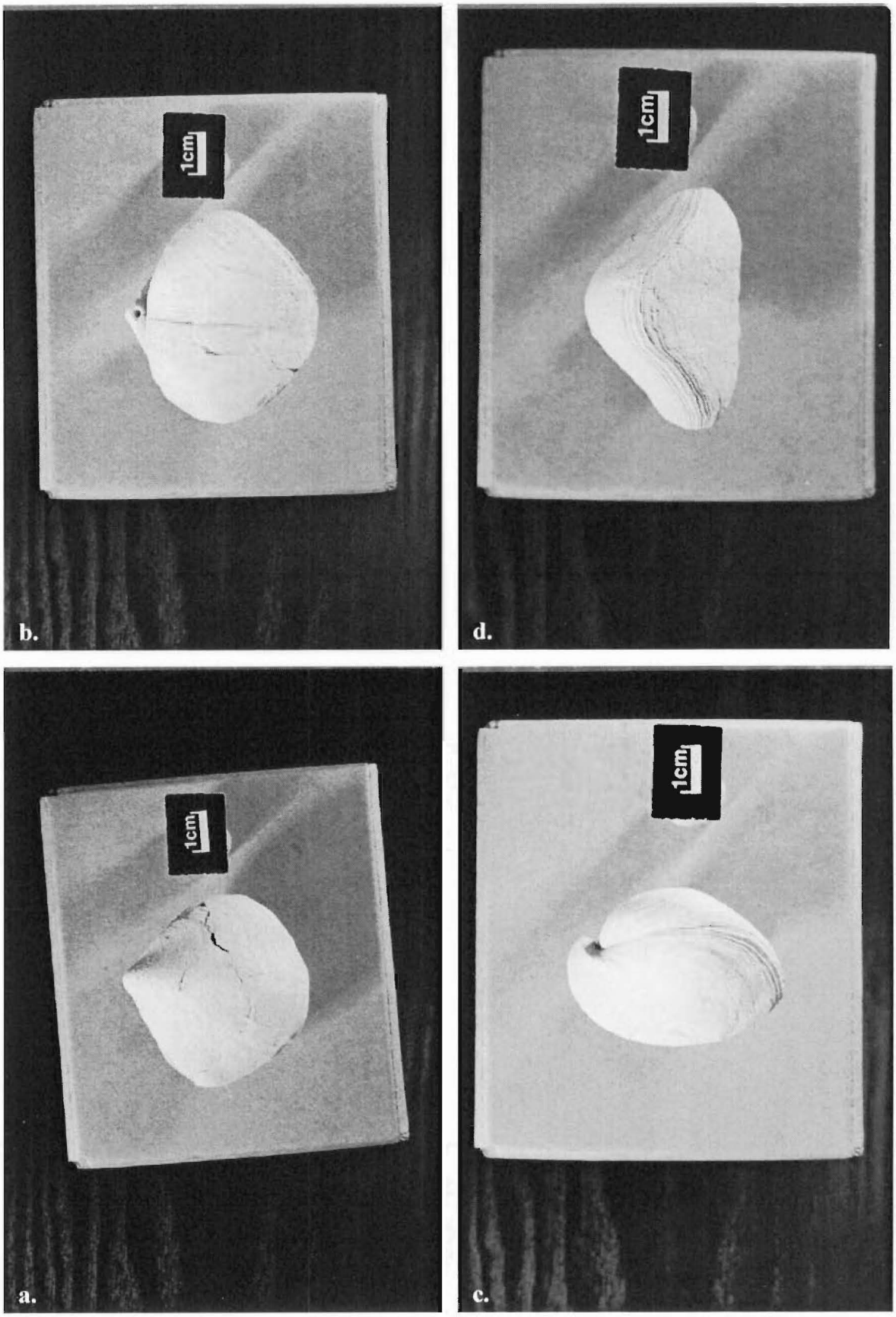


Figure 71. Holotype of *Pachymagas balfourensis* (UCM 1473).

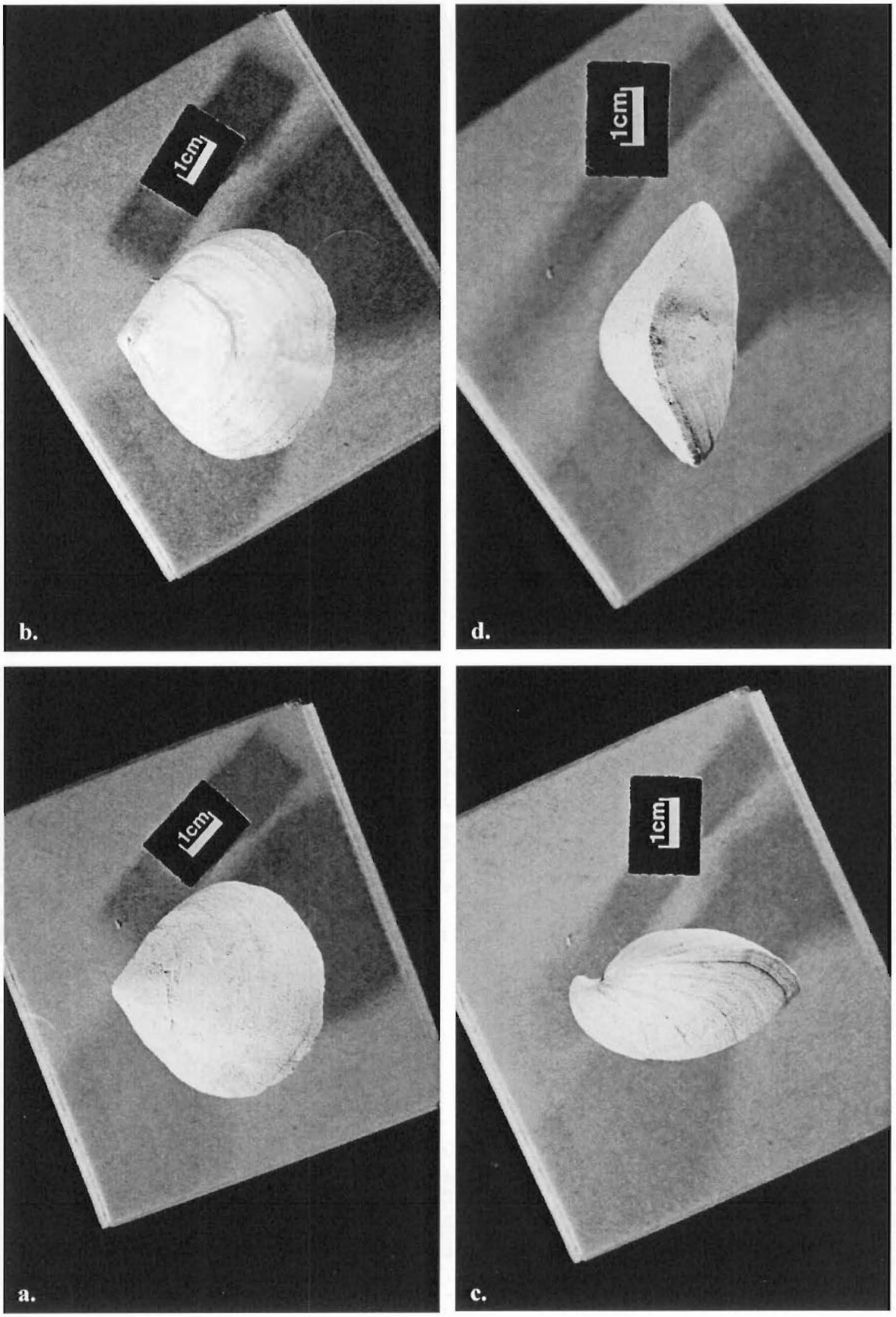


Figure 72. *Pycnozygus triangularis* (Allan Colln. 26048) from Balfour Quarry.

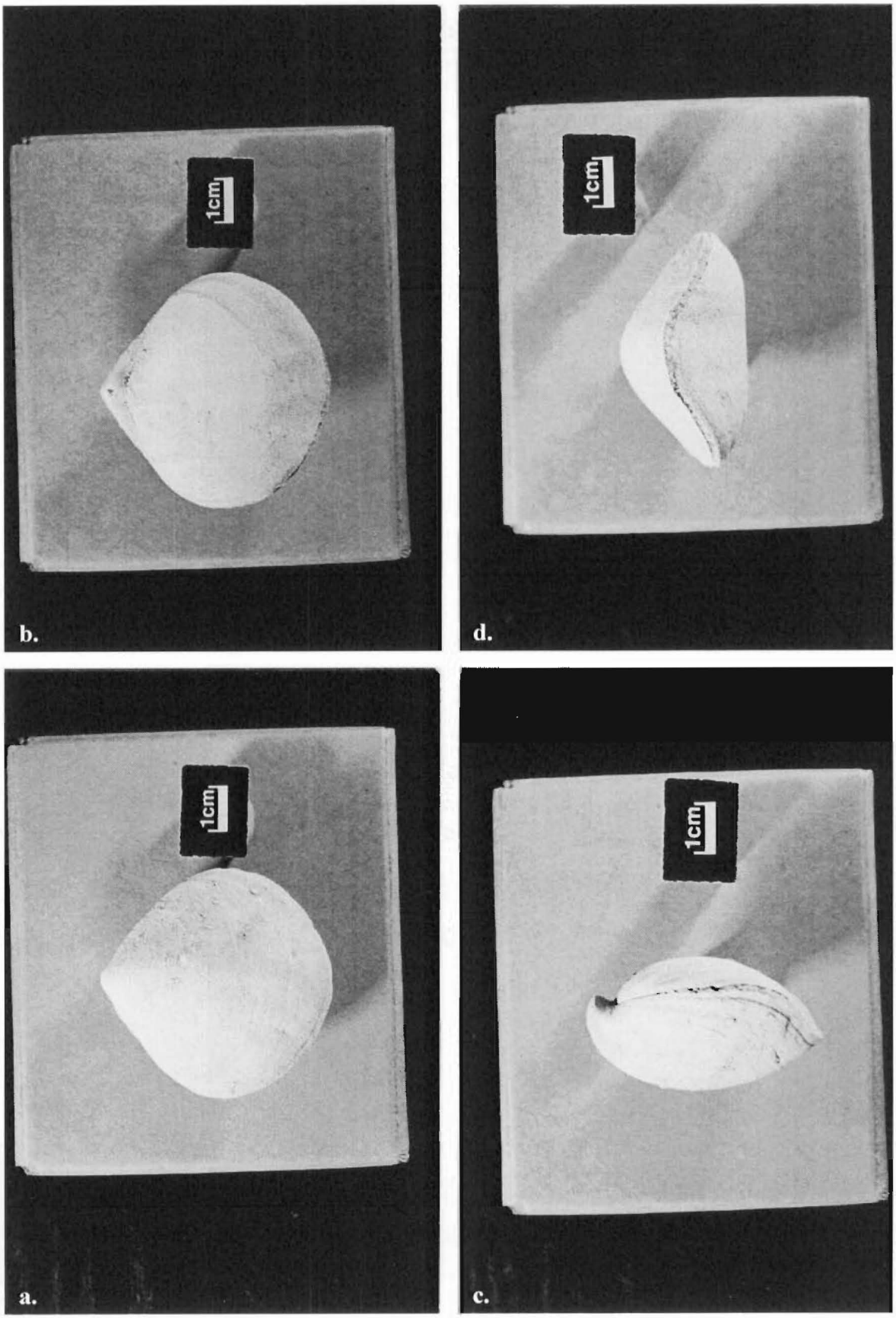


Figure 73. *Pycnozygus triangularis* (Allan Colln. 26013) from Balfour Quarry.

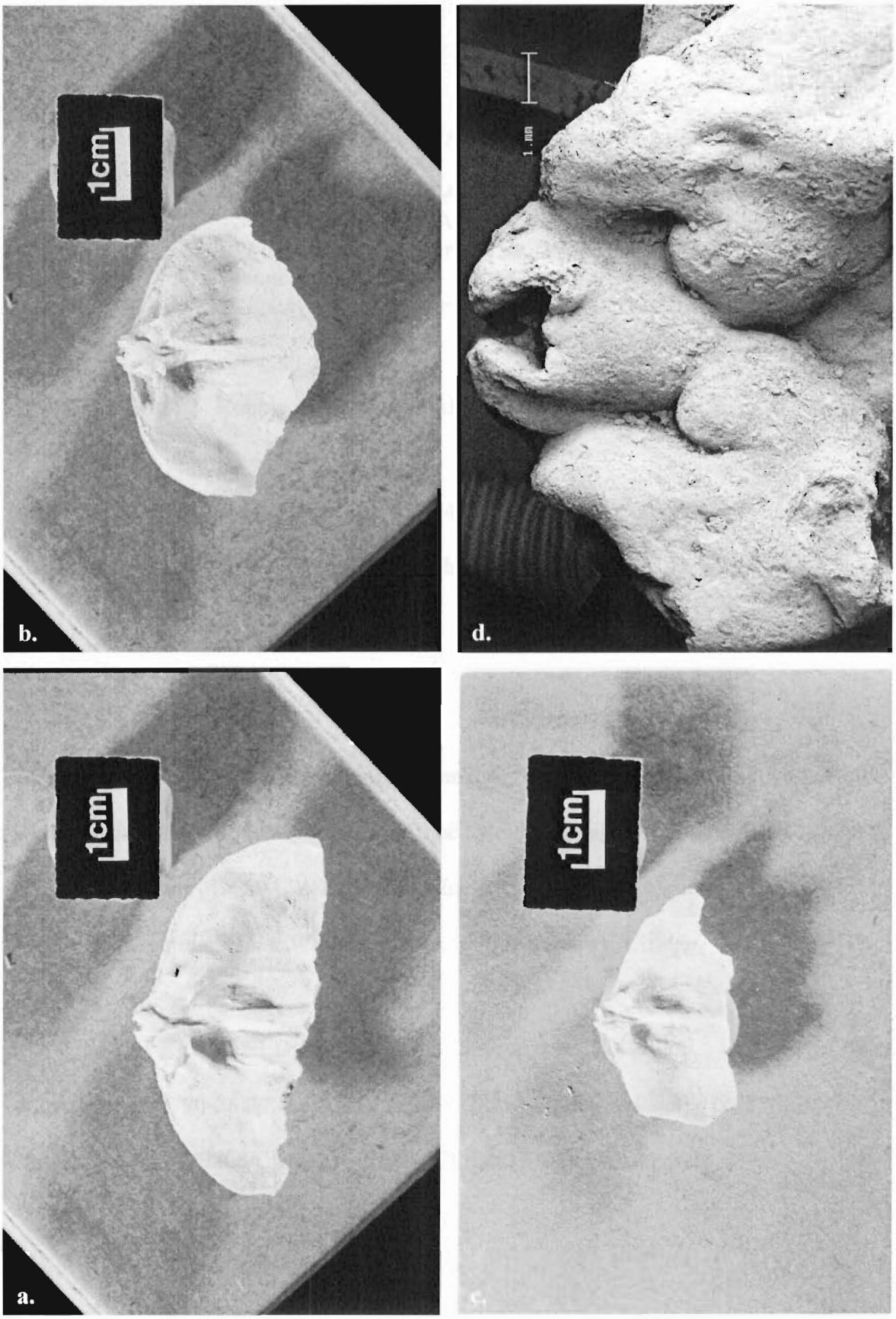


Figure 74. Dorsal interiors for paratypes of *Pachymagas balfourensis* (**a**, **b**, **c**: UCM 1474) and dorsal interior of *Pycnozygus triangularis* (**d**: Allan Colln. 26025) from Balfour Quarry.

3.13 *Pycnozygus turneri* (Allan, 1931)

SYNONYMY:
Pachymagas turneri Allan, 1931, p. 158-159, pl. 21, fig. 1, pl. 22, figs. 8-10
Pachymagas turneri Allan, 1937c, p. 136
Stethothyris epsilon Allan, 1940 (in part), p. 289
"*Pachymagas*" *turneri* Allan, 1960, p. 246, 265 (stratigraphic range)
"*Pachymagas*" *turneri* Dawson, 1990a, p. 71-72

TYPE LOCALITY: Rubbly limestone, Clifden Quarry, Clifden, Southland.

TYPE MATERIAL: Holotype (UCM 1477) in the Department of Geological Sciences, University of Canterbury, Christchurch.

(Source: Dawson 1990a)

OCCURRENCE: Takaka Limestone {Nelson}, of: Takaka and Aorere Valleys, north-west Nelson; Main Mount Brown Limestone (Mount Donald horizon of Allan 1937c) {North Canterbury}, at: Weka Pass; Sharks Tooth Hill Member, Forest Hill Formation {Southland}, at: Waiau River and Clifden Quarry, Clifden.

MATERIAL EXAMINED: Material in the Allan Collection, University of Canterbury: (28790-28828 Takaka) ; (28832-28854, 28862 Takaka) ; (28870, 28875-28877 Takaka) ; (29208 Clifden) ; (26287 Clifden) ; (26949? Deborah).

AGE/RANGE: Waitakian – Altonian

FIGURES: 75-77

DESCRIPTION: Large, smooth, biconvex shell displaying numerous faint growth-lines; shell broadly ovate, almost suborbicular, the ventral valve relatively inflated; cardinal margin gently curved; anterior commissure weakly very broadly unisulcate. Beak obtuse, attrite, erect to incurved; fairly small circular mesothyrid foramen; beak ridges variable – usually well rounded and ill defined, though frequently angular and well defined; convex cardinal area with high, broad symphytium, rare adult specimens retaining traces of original conjunct deltidial plates, fused anteriorly. Median septum fairly slender, rising from a thickened base on the valve floor and extending anteriorly about one-third of valve length, bifurcating posteriorly to unite with the hinge-plates, forming a v-shaped hinge-trough with shallowly inclined walls; crural bases fused to thickened inner socket ridges. Substantial thickening and infilling of the hinge-trough in adults partly obscures the (juvenile) relationships between elements of the cardinalia. Cardinal process consisting of roughened myophore with an anterior rounded lobe and lateral rim extending posteriorly, together forming a cup-shaped platform in the centre of which the diductor muscles attached. The lateral rims are folded up almost overtop of the cup-shaped depression; the crural bases and inner socket ridges show signs of fusing medially with the swollen cardinal process, itself occupying over half of the hinge-trough, the pedicle adjustor muscles confined to shallow depressions either side of the lobe of the cardinal process. Dorsal adductor muscle scars are large, terminating anteriorly at approximately the termination point of the median septum – at one-third the length of the valve, but may rarely extend further. Adult loop teloform.

DISCUSSION: In Allan's (1931) original description of *Pachymagas turneri* the interior characteristics were not noted, as only two specimens of the species were

known. Allan (1931, p. 159) stated "*P. turneri* n. sp. is a very distinct species which does not seem to be closely related to other members of the genus known from New Zealand". Allan (1937c) later recorded a further single specimen from the Mt. Donald horizon at Weka Pass, noting its rarity there.

The species is indeed very distinctive exteriorly, somewhat resembling somewhat juveniles of *Stethothyris epsilon*, a species Allan (1940, p. 289) seems to have mistaken *Pycnozygus turneri* for in the Takaka Limestone. Interiorly the species resembles *Pycnozygus triangularis*, though elements of the cardinalia are slightly less swollen, resembling the juvenile cardinalia of *S. epsilon* (fig. 77). The beak normally is not incurved as is the beak of *S. epsilon*, though does resemble juvenile *S. epsilon* in this respect (fig. 76). *Pycnozygus turneri* occurs in Altonian strata at Weka Pass and Clifden. *Stethothyris epsilon* occurs at Weka Pass, according to Thomson (1920) and Allan (1960), in the calcareous sands at the base of the "E" limestone of Thomson (1920) – the Main Mt. Brown Limestone Member of the Mt. Brown Formation, of Altonian age (Browne & Field 1985). However, at Weka Pass *S. epsilon* occurs most conspicuously in the "Hinnites shell-bed" (Thomson 1920) at the base of the Glenmark Limestone Member – of Waiauan age (Browne & Field 1985). At Clifden *Stethothyris epsilon* occurs in strata of Lillburnian age (Fleming et al. 1969). McCulloch (1981) was unable to locate any additional *Stethothyris epsilon* from the calcareous sands at the base of the "E" limestone, and noting that Thomson's (1920) record of *Stethothyris epsilon* from the sands was made from the base of the scarp slope of the Glenmark Limestone Member, proposed that Thomson's record may represent material that weathered out of the stratigraphically higher (and younger) "Hinnites shell-bed" to lie at the base of the scarp slope, from where Thomson

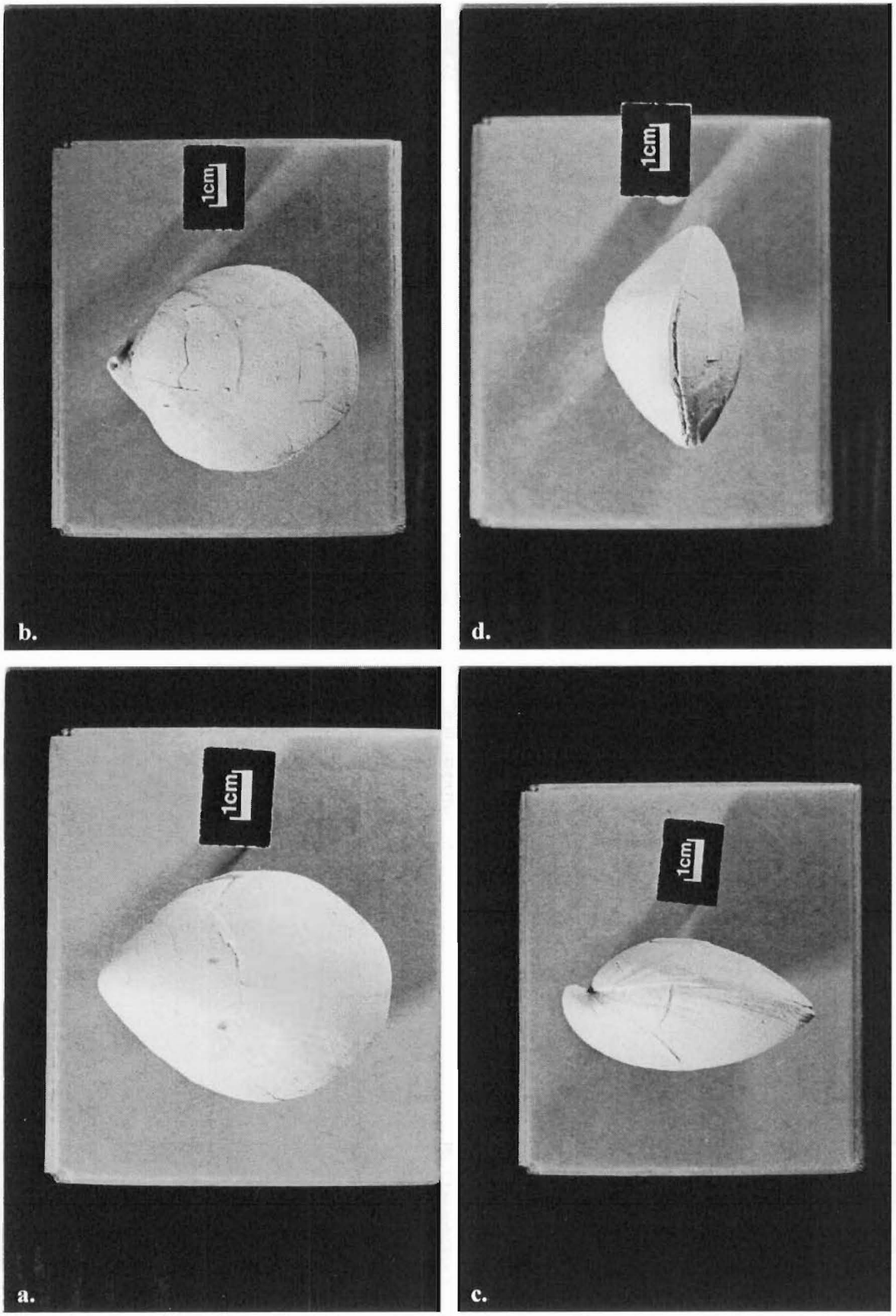


Figure 75. Holotype of *Pachymagas turneri* (UCM 1477).

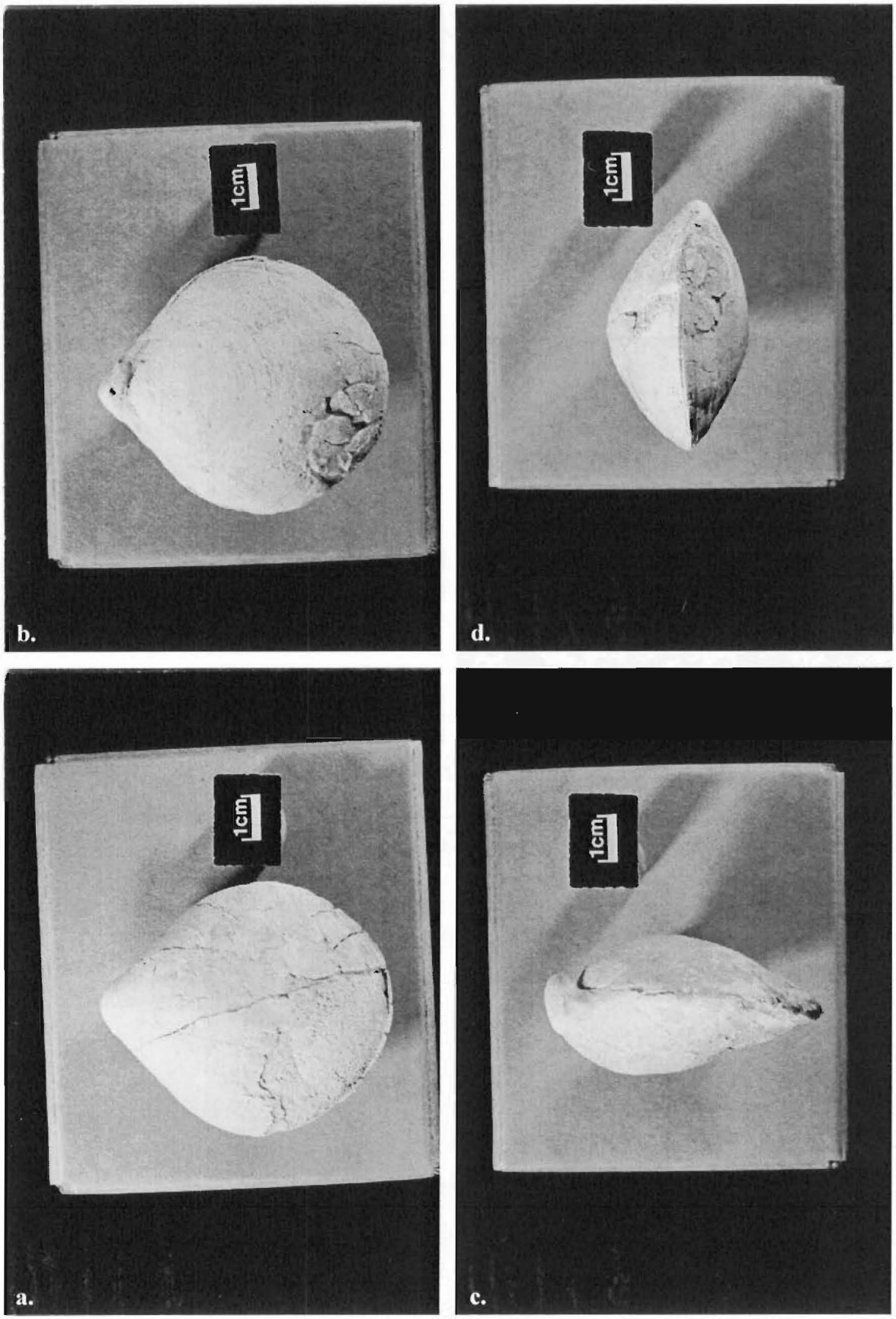


Figure 76. *Pycnozygus turneri* (Allan Colln. 26287) from Clifden.

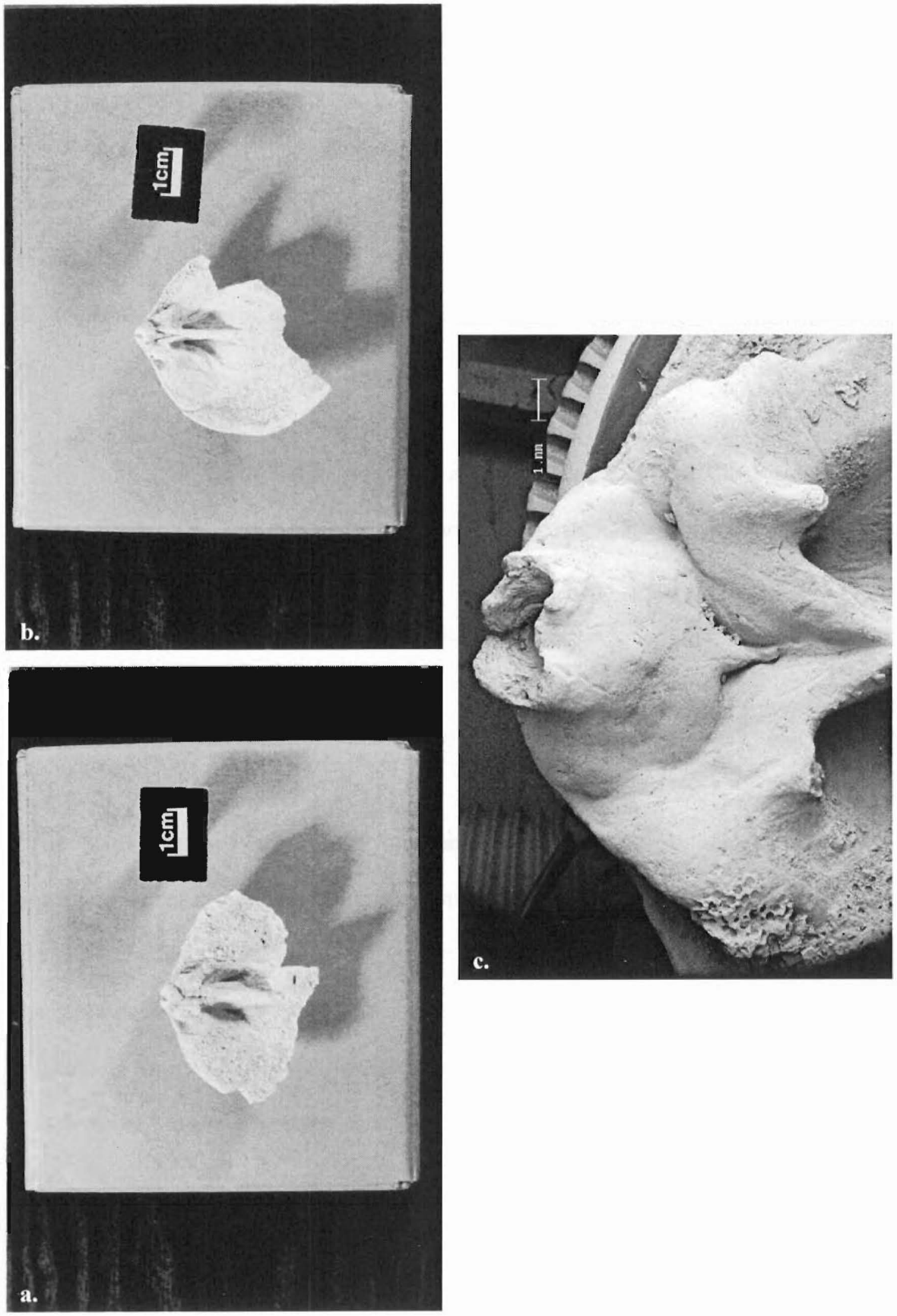


Figure 77. Dorsal interiors of *Pycnozygus turneri* (**a**: UCM 2013; from Takaka; **b**: Allan Colln. 29208; from Clifden; **c**: UCM 2012; from Clifden Quarry).

collected. Hence McCulloch speculates that Thomson's record of *S. epsilon* from the calcareous sands may be based on material that was not *in situ*. Alternatively, Thomson could conceivably have misidentified the externally similar *Pycnozygus turneri*, recording it as *S. epsilon* from the calcareous sands. There is, however, no evidence that *P. turneri* occurs any higher than the Mt. Donald horizon (Allan 1937c) at Weka Pass, an horizon a significant distance below the calcareous sands themselves (fig. 11).

Noting its stratigraphic proximity at both Weka Pass and Clifden, and its interior similarities, it is proposed that *P. turneri* gave rise to *S. epsilon*.

INCERTAE SEDIS

3.14 *Pachymagas* (?) *uttleyi* Allan 1937

This species is only known from the holotype (fig. 78), additional specimens not found amongst material examined from Ward's Quarry, the type locality. Allan (1937d) remarked that the species resembles *Neothyris* (?) *anceps* in possessing a high symphytium, wide lateral palintropes and a large foramen. The specimen, however, is moderately unisulcate, where *Neothyris* (?) *anceps* is typically near rectimarginate, and does not possess a foramen as large as seen in *anceps*. It is a difficult species to place, the interior characteristics being unknown, and it could possibly be a large well developed specimen of *Waitakia bartrumi*, common in the Forest Hill Limestone of Southland, and occurring at Ward's Quarry at a position stratigraphically slightly lower than that from which *P.* (?) *uttleyi* was recorded (Allan 1937d). However, it could be said to more closely resemble *Neothyris* (?) *anceps*, a species itself in need

of systematic revision and assignment to a new genus (Allan 1960). For these reasons the species is classified as *incertae sedis*.

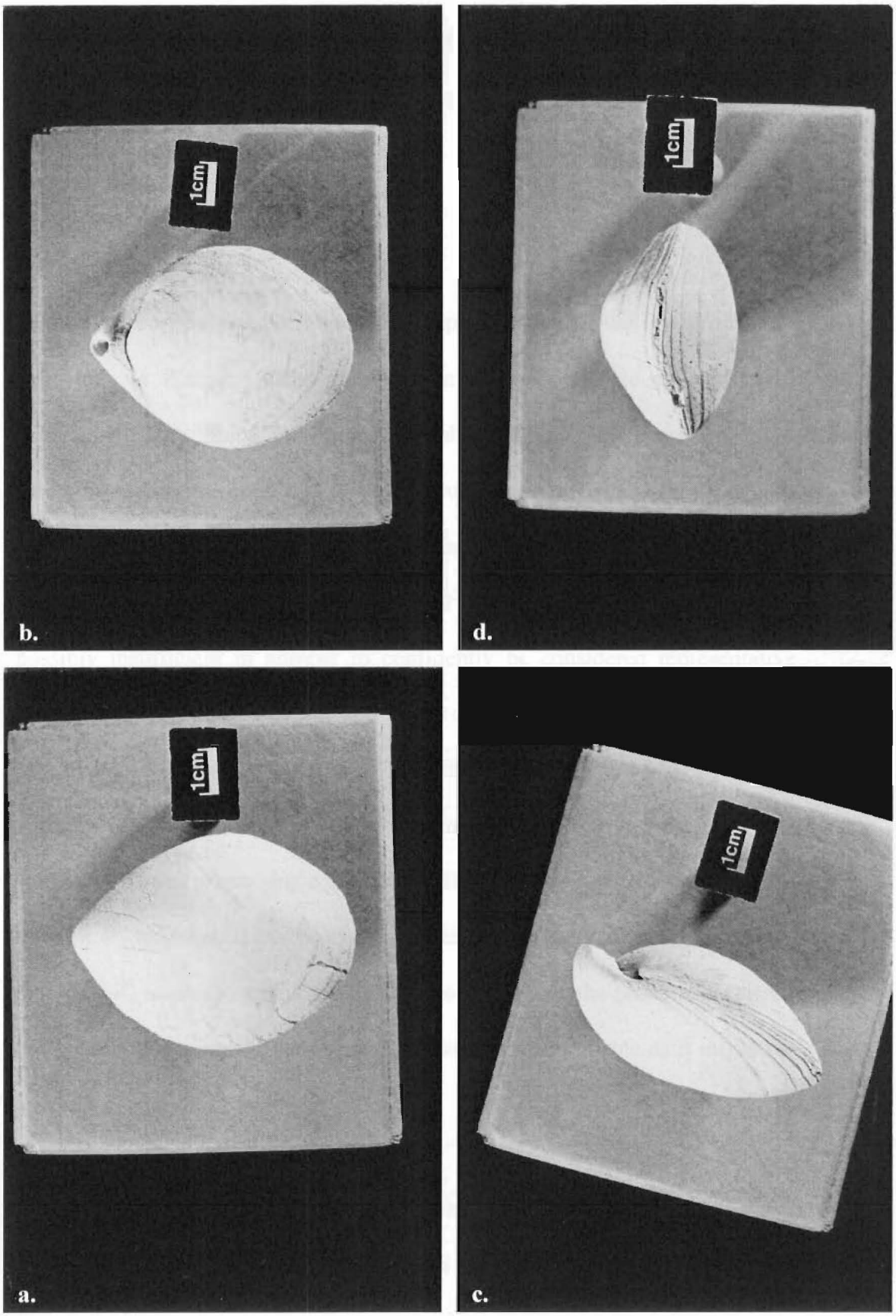


Figure 78. Holotype of *Pachymagas* (?) *uttleyi* (UCM 1667/Allan Colln. 1210).

Chapter Four:

' Discussion and Conclusions'

4.0 Discussion

The earliest *positively* identified representative of the two primary genera of this study is *Waitakia elliptica*, found in Duntroonian age strata. Material from Wharekuri Creek, thought to have been collected from Whaingaroan age strata, was examined during the course of this study but was not satisfactorily identified, though it is thought that the species present is either *Waitakia elliptica*, *Waiparia abnormis*, or the (unidentified) Whaingaroan ancestor of both genera. While the specimens are possibly insufficient in number to confidently be considered representative of the species found at the locality, the specimens do appear to display consistent possession of a hypothyrid foramen and beak characteristics reminiscent of *W. abnormis*, while interiors resemble those of *W. elliptica* from Squires Farm, having very thickened cardinalia though possessing a smaller cardinal process than is characteristically seen in adult *W. elliptica*. It has been determined during the coarse of this study that the record of *W. abnormis* extends back into the Waitakian; the possible occurrence of *W. abnormis* in Whaingaroan strata does not seem as improbable as it might have done previously, in light of this fact.

While Thomson (1920) suggested derivation of both genera from a presumably Duntroonian or older common ancestor, noting the possibility *Waitakia elliptica* (*Pachymagas ellipticus*) may have arisen through direct descent from *Waiparia*, it is thought that *W. abnormis* could equally well have evolved from *W.*

elliptica, though, broadly speaking, the *Waitakia* lineage consists of "a sequence of increasingly more peramorphic species" – a peramorphocline (McKinney & McNamara 1991, p. 149). Though *Waiparia* isn't part of the *Waitakia* lineage *per se*, its descent from *Waitakia elliptica* might *seem* less likely when it is considered that descendant species of the 'main' lineage are all peramorphic, not paedomorphic as *W. abnormis* would have to be held in the case of descent from *W. elliptica*. Whether or not such development should be considered 'less likely' is open to question. Retention of the juvenile beak characteristics of *W. elliptica* in descendent adult *W. abnormis* (paedomorphosis) adequately explains the origin of the genus, though the primitive cardinal process observed in *one* (of the two known specimens from the Concord Greensand at Seacliff) specimen from the Waitakian Concord Greensand possibly suggests that *W. abnormis* exists in a more primitive state of morphological development than does *W. elliptica*, suggesting rather a derivation from some earlier, pre-Duntroonian form. The Wharekuri Greensand must be recollected in aid of establishing the origins and early evolution of both genera. In regards to evolution in the genus *Waiparia*, it can be stated with certainty that *W. intermedia* arose through peramorphosis from *W. abnormis*, displaying a change from relative isometric growth to allometric growth with a resulting shape change to a more suborbicular exterior shell morphology.

The origins and affinities of *Waitakia* (?) *trelissickensis* remain in doubt, its occurrence in Duntroonian or Waitakian strata (see section 3.11) suggesting evolution from *Waitakia elliptica*. The exterior morphology of *trelissickensis* is very different from that of *elliptica*, due, no doubt, to adaptation for occupation of the marine basaltic tuffs in which it is found. Interiorly the species demonstrates characters that

are not inconsistent with possible evolution from *W. elliptica*. This species exteriorly resembles *Neothyris* (?) *anceps*, and may be an early representative of that species.

The origins of *Waitakia marshalli* are elucidated when the juvenile form is compared with juveniles of *Waitakia elliptica*. The juveniles of both species look very similar, having in the past been mistaken, one for the other (e.g. Allan 1940). They can be discriminated however, as the hinge-line of *W. elliptica* is only wide in very small juveniles, but the hinge-line is wide in juveniles and adults of *W. marshalli*. The foramen is much larger in juveniles of *W. marshalli* than in similarly sized juveniles of *W. elliptica* also. These characters are peramorphic relative to those of *W. elliptica*, shell size being peramorphic relative to shell size in *elliptica*.

Whether the changes seen proceeding from *W. elliptica* to *W. marshalli* are truly evolutionary or merely ecophenotypic is a difficult matter to determine for certain. It has been suggested in discussion of *W. marshalli* (section 3.9) that the species formally known as *Pachymagas clarkei* Thomson is actually an ecophenotype of *W. marshalli*. However, it is possible to consider that *W. marshalli* is actually an ecophenotype of *W. elliptica*, and the 'ecophenotype' *Pachymagas clarkei* actually represents re-emergence of the developmental program for controlling expression of the *W. elliptica* morph – i.e. *W. marshalli* is an ecophenotype of *W. elliptica* which, when it finds its way into the environment in which the White Rock Limestone was deposited, demonstrates a reversion to (or a re-emergence of) the underlying developmental program (for the species *W. elliptica*), previously perturbed by environmental factors (hence the *W. marshalli* morph). Though the proposed 'return to the underlying developmental program for *W. elliptica*' seen in *Pachymagas clarkei* does not in fact demonstrate a return to the *W. elliptica* morph, as it should, it

can be suggested that this is so because the environment in which the White Rock Limestone was deposited and in which *Pachymagas clarkei* lived is not the same as the environment in which the Kokoamu Greensand was deposited and in which *Waitakia elliptica* lived. Comparison of morphologies seen from 'equivalent' environments is necessary. To this end consideration is directed toward another suggested ecophenotype of *W. marshalli* (see discussion in section 3.9) which occurs in the Berrydale Greensand overlying the Otekaike Limestone at Curiosity Shop. This ecophenotype's resemblance to *W. elliptica* is close, and one would have to cite similarity in the environment of deposition for the Kokoamu and Berrydale Greensands to explain it. The resemblance is not exact (e.g. the foramen is typically larger than seen in equivalently sized specimens of *W. elliptica*) and it can be argued that the general morphology seen in the lineage (and in terebratellids in general) is so similar that equivalence of species cannot be based solely on this near equivalence of shell exterior – but interiors of the 'ecophenotype' from Curiosity Shop resemble interiors of *W. elliptica* proper also.

It seems certain that the persistence of the *W. marshalli* morph from Waitakian into Otaian times would require the alterations to the developmental program to have become genetically fixed, especially considering that *W. marshalli* with a 'typical' morphology occurs in a variety of lithologies (and by inference environments) – i.e. Otekaike Limestone, Bluecliffs Siltstone, Caversham Sandstone. This considered, the suggested 'ecophenotypes' probably are due to real ecophenotypic response, rather than the highly speculative theory of return to the unmodified or 'default' developmental program.

It is probably not by coincidence that the suggested ecophenotype (above) of *W. marshalli* which occurs in the White Rock Limestone resembles the descendent species of *marshalli* in Oamaru – *Waitakia haasti*. Similarities observed in exterior and interior characters probably owe their origins to similarities of habit within dissimilar environments, as equivalence in depositional environment cannot be suggested for the White Rock Limestone and Gee Greensand. While *W. haasti* is considered a descendent of *W. marshalli*, not related to the ecophenotype seen in the White Rock Limestone, it could *conceivably* be the case that *W. haasti* represents the descendent of this ecophenotype in which the ecophenotypic expression has become genetically fixed, and hence considered a separate species rather than an ecophenotype. However, as the occurrence of the White Rock Limestone 'ecophenotype' and *W. haasti* are in geographically disparate locations, and no specimens resembling them have been found elsewhere, it is considered that they are not related.

Evolution from *W. marshalli* then proceeds along two differing pathways, one leading to the populous brachiopod horizons in the Main Mt Brown Limestone of Weka Pass and the Forest Hill Limestone of Southland, and the other to the various brachiopod horizons seen in the greensands of Oamaru. Where the Otekaike Limestone gives way to Waitakian aged Gee Greensand in Oamaru (i.e. Gee's Point; Kakanui), it is observed that the exterior morphology of the representative *Waitakia* species has changed from strongly biconvex (as seen in the ancestor *W. marshalli*) to weakly biconvex, requiring recognition of a new species – *Waitakia alldayi*. Interiorly the species in this lowest level of greensand seems fairly primitive, but this is thought to be an initial response to the newly occupied habitat (see section 3.3). At slightly

higher levels the species in the greensands, while still being weakly biconvex, has developed interiorly, having a steep walled hinge-trough and other advanced characters (see section 3.3). The Gee Greensand gets progressively more muddy with stratigraphic height (fig. 18), and it is possible that the continued expression of the weakly biconvex morphology, in contrast to that seen in contemporary? *W. haasti* of the cleaner, siliciclastic poor Gee Greensands, is due to a difference in substrates.

Waitakia haasti, while possibly having evolved from *W. alldayi*, probably owes its origins, like *alldayi*, to evolution from *W. marshalli*. However, specimens that are found in the *basal* Gee Greensand (see above) are referred to *W. alldayi* by virtue of their weakly biconvex nature, and general overall resemblance to the specimens found at the type locality, All Day Bay. The origins of *W. haasti* quite possibly lie with these specimens which mark a re-occupation of greensand forming environments by *Waitakia*.

Waitakia parki occurs in stratigraphically higher and younger strata than does its ancestor, *W. haasti*. The two species differ most evidently in degree of sulcation of the shell, *W. parki* being markedly more sulcate than *haasti* (and all other members of the genus). The species also differ interiorly, *W. parki* demonstrating more posterior thickening and peramorphic development of the cardinal process relative to *haasti*, a 'result' of its position further along the aforementioned *Waitakia* peramorphocline.

In Altonian strata at Weka Pass and in Otaian strata of at least two Southland localities (Doherty's Quarry and Lady Barkly Quarry) the large inflated species *W. cottoni* is found. *Waitakia cottoni* is exteriorly very similar to *W. marshalli*, being suborbicular and strongly convex, and is interpreted to have evolved from *W.*

marshalli in the Otaian. Specific differences are seen interiorly, where commonly *cottoni* demonstrates hinge-plates that are (becoming) discrete of the septum, not medially fused to it as in all older species and in *W. parki*. Hyden (1979) suggested that the size difference seen between specimens from such localities as Lady Barkly Quarry and Forest Hill can be interpreted with reference to differences in lithology – the fauna at Forest Hill occurring in a bioclast rich carbonate mud while that at Lady Barkly occurring in a glauconitic muddy sand substrate (Hyden 1979, p. 236). Hyden interpreted this as possibly indicating that rate of sedimentation (presence of glauconite) had a control on the size of the shell, slow deposition rates leading to larger sizes. Cooler temperatures might also have led to larger shell sizes (Hyden 1979, p. 236). Presumably the shape differences seen between specimens from Lady Barkly Quarry and Forest Hill are explained with this model, though Hyden didn't specifically state this. It is considered in this study that the large suborbicular brachiopods seen at Weka Pass, Waihi River, and at the Lady Barkly and Doherty's quarries are specifically distinct from those stratigraphically higher forms, which are referred to *Waitakia bartrumi*.

Waitakia bartrumi, like *W. cottoni*, possesses hinge-plates that are becoming discrete of the median septum. In common with that species it possesses a symphytium, the beak being suberect rather than erect as in *cottoni*. The species demonstrates an inversion from suborbicular to elongate elliptical shell shape, which parallels the change in lithology type at Weka Pass – from the underlying sands to the Main Mt Brown Limestone proper. Occupation of this sandy substrate probably required an utilisation of the suborbicular shape seen in *cottoni* as a stability mechanism, the posterior weighting of the shell providing further stability.

Presumably this shape was lost in evolution of *W. bartrumi* as it wasn't required for occupation of the coarse calcareous sands of the Main Mt Brown Limestone.

It has been suggested (section 3.5) that the *W. bartrumi* bearing horizons of the Main Mt Brown Limestone and the Forest Hill Limestone of Southland possibly differ in age, the specimens from the Main Mount Brown Limestone being the older as certain characteristics such as beak curvature don't seem as 'advanced' (though here a suberect beak with a high symphytium is considered advanced, an erect beak with a small compressed symphytium or conjunct deltidial plates primitive), the specimens being of a smaller overall size. Possibly specimens from Southland are merely geographic variants of the same age as specimens from the Main Mt Brown Limestone. Differences in local temperature could possibly account for the observed size contrasts, the specimens of Southland possibly growing for a longer time, therefore being more morphologically advanced than those specimens from the Main Mt Brown Limestone. It is considered, however, that this theory cannot adequately explain the larger number of specimens with suberect beaks seen in Southland, as the change from erect beak to suberect beak in the lineage is an evolutionary one, not a result of growth. Hence, specimens of *W. bartrumi* from the Forest Hill Formation of Southland are considered younger than those from the Main Mount Brown Limestone.

Specimens of *W. bartrumi* found at Clifden from the Nga Pari Formation come from uppermost Altonian strata, and it is almost certain that *bartrumi* occurs at higher stratigraphic levels than this recorded occurrence, as the descendent species *Neothyris* occurs at Clifden in strata of Lillburnian ages. This is the earliest recognised occurrence of *Neothyris*, the loss of the transverse connecting band in *Waitakia* requiring reference to that genus. While some specimens from Clifden

demonstrate that the transverse connecting band was in the process of being lost by the genus, it probably was not fully lost until Clifdenian times.

The odd species *Waitakia andrewi* occurs in the calcareous sands above the horizon in which *W. bartrumi* is found at Weka Pass. The suborbicular shape and the beak characters of some specimens of the species probably suggests derivation from *W. cottoni* rather than *W. bartrumi*. *Waitakia andrewi* seems to be a species in which the pedicle atrophied significantly, and which lay passively on the substrate with the suborbicular shell shape providing significant support, the posterior weighting of the shell holding it in a stable position.

Interpreted phylogenetic relationships for the species of *Waiparia* and *Waitakia* are illustrated in figure 79.

4.1 Conclusions

This study set out to reinvestigate speciation in the genera *Waiparia* and *Waitakia*, and to outline the phylogenetic relationships between the constituent species of both these genera. Measurements of shell parameters such as length and width were taken in an effort both to quantify variation, and to determine if any statistical differences existed between collections from various localities, differences that might help in species discrimination. Interiors were excavated and examined where possible, in an effort to deduce species characteristics. Photographic illustrations were made using a Scanning Electron Microscope for the interiors of most species, the exteriors being illustrated with conventional photographs.

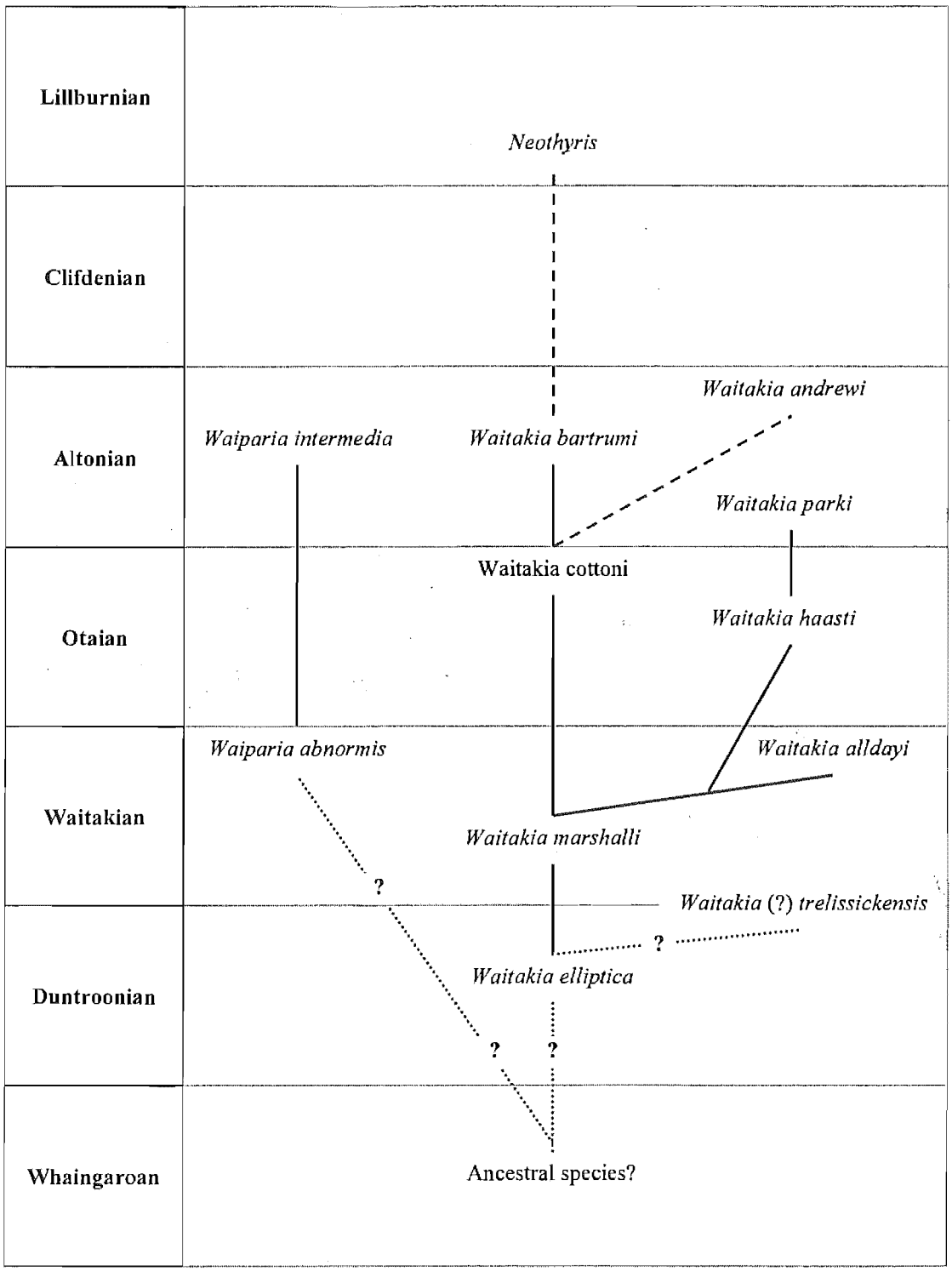


Figure 79. Interpreted phylogenetic relationships for *Waiparia* and *Waitakia*. Full lines represent established relationships, dashed lines represent inferred relationships, and dotted lines represent uncertain relationships. The species are placed as at their first occurrence in relation to the time-scale – e.g. *W. abnormis* first occurs in the Waitakian, the species placement on the chart represents this, but it should be remembered that *W. abnormis* ranges into the Altonian.

Ultimately, arbitrary judgements have to be made in determining what precisely constitutes a fossil species, based on what the above outlined procedures bring to light. Statistical techniques were not relied upon to determine any of the species of this study, as statistical data was only obtainable for a few localities, frequently specimens being unsuitable for measurement or too few in number to be statistically representative of fossil populations. Additionally, statistical tests demonstrate statistical differences between localities and populations, not necessarily biological differences (Hyden 1979). Even through examination of morphological characters it was difficult to determine what was and was not a species or an ecophenotype, as the variability seen in both *Waiparia* and *Waitakia* was high, and blurred genotypic identity somewhat.

Examination of interiors for the species that are here established shows that changes between the species are not large, and are gradational – reflecting the gradualistic evolution of the lineage. This, too, compounded initial species recognition, painstaking excavation uncovering yet 'more of the same' in every direction. Excavation was vital, however, as many of the species established by J. A. Thomson and by R. S. Allan were never examined interiorly, and, if nothing else, needed to be illustrated. However, a new species of a recently recognised new genus, *Pycnozygus* Hiller & MacKinnon, was brought to light through excavation. The procedure must be considered a success in this these terms.

It has to be emphasised that the results of this study, more than anything, are an *interpretation* of speciation and evolution for those forms studied. Thomson and Allan have both been criticised for following a typological species philosophy, and for not recognising variation within species. The author could perhaps be criticised for

going too far the other way – "lumping" species, rather than "splitting" them. Foster (1974; 1989) suggested that many fossil species, especially those with limited geographic ranges are probably artificial, resulting from oversplitting, many modern species demonstrating wide geographic ranges. The nine species of *Waitakia* described in this study were previously assigned to 24 species by Thomson and Allan. Four of the nine recognised species have relatively wide geographic ranges, with the rest being confined to areas relatively close to their type localities. Many of Thomson's and Allan's species may nominally have had wide geographic ranges, but the difficulty of identification of their 'closely related', almost morphologically identical species casts doubt on the validity of interpreted geographic ranges.

It is therefore considered that the results of this restudy present a species framework for *Waitakia* and *Waiparia* that works, is in accord with modern geographic species ranges, and is simple. The species framework is both simple in application and in underlying philosophy, seeking to explain observations in the simplest (acceptable) manner possible – hence the bulk of the species described by Thomson and Allan are interpreted to be phenotypic variates of a few species within the phenotypically plastic genus *Waitakia*.

4.2 Future Work

Apart from further collection in general from all localities, and integration with paleoecological reconstructions for important brachiopod bearing units of the study, a number of options for future work exist, and are outlined below.

4.2.1 This study did not determine the origins of the *Waiparia-Waitakia* lineage, a very few specimens from the Wharekuri Greensand hinting that the origins may lie within that lithology, awaiting discovery. New collections must be made from this lithology, and old collections re-examined in aid of establishing the early origins of this lineage.

4.2.2 An effort to determine the stratigraphic range of *W. abnormis* and *W. intermedia* could demonstrate whether the species are truly specifically separable, or whether, through lack of data, two species have been created where only one is required.

4.2.3 Future collecting at localities where ecophenotypes have been considered to occur, such as in tuffaceous lithologies of the Brothers Volcanics in South Canterbury, along with detailed paleoecological reconstructions would no doubt prove whether these ecophenotypes are real or imagined, and what they represent.

4.2.4 Examination of *Waitakia* (?) *trelissickensis* in parallel with a restudy of *Neothyris* (?) *anceps* is required to confirm or rule out an ancestor-descendent relationship between the two species.

4.2.5 An analysis of the transition from *Waitakia* to *Neothyris* by loss of the transverse connecting band through examination of material from Clifden might help to determine more accurately the time at which this process occurred, and, in parallel with examination of material from the Main Mt Brown Limestone and overlying sands, whether this process could have occurred more than once.

4.2.6 Excavation of *Waitakia andrewi* from Weka Pass and figuring of interiors would complete the photographic record for the species, and the genus as a whole.

4.2.7 Outside of New Zealand, specimens of "*Pachymagas* cf. *cottoni*" described by Biernat et al. (1985) probably need reassignment to the genus *Waiparia*.

Acknowledgements

I acknowledge the assistance of the following people:

Dr. David MacKinnon for Supervision, discussion, and guidance. Elliot Dawson for encouragement and for providing me a personal copy of his "The Cenozoic Brachiopoda of New Zealand" which proved truly invaluable. Dr. Kerry Swanson for developing and printing a great many negatives. Dr. Norton Hiller for assistance with Canterbury Museum material and helpful discussion. Jane Guise for help with practical work of all kinds. John Southward for help with computers and computing matters. Dr. Daphne Lee for providing me access to the Otago University brachiopod collection. Craig Jones for much assistance at the beginning of the project. Dr. Bruce Marshall for assistance with National Museum of New Zealand material.

Appendix

Brachiopod Measurements

(numerical measurements are given in millimetres and in degrees)

Weka Pass

Italicised entries are approximate due to slight crushing of shell etc.

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
368	23.3	20.6	10	19.2	12	1.9	98	13.7	1.2	mesothyrid	2.5	0.5
369	29	25.9	13.8	26.7	15	2.2	99	17		mesothyrid	2	1
370	39.1	34.6	21.4	30.2	21.4	2.9	100	22.4		mesothyrid	2	2
371	29.4	25.9	16.6	25.4	16.4	2.2	114	19	1.2	mesothyrid	3	1.5
372	34.8	30.8	19.3	30.8	18.4	2.5	109	21.2		mesothyrid	3	3
373	36	31.5	*19*	28.7	19.2	2.9	103	21.3	1.5	mesothyrid	2	3
374	33	29.4	16.1	27.7	16.5	2.3	105	18.6	1.4	mesothyrid	3	1.5
376	38.7	34.2	19.3	29.6	21.3	3.3	93	22	1.3	mesothyrid	3	3
378	37.6	33.9	17.8	34.1	19	2.5	106	22.5	1.5	mesothyrid	2	2
379	37.3	33.4	19.7	28.1	22.3	2.3	89	19.1	2.4	mesothyrid	2	2
388	29.3	26.8	16	25.1	16.2	1.7	101	16.4	0.7	mesothyrid	3	0.5
389	27.9	25.1	15.1	*23*	14.3	1.7	105	16.9	1.1	mesothyrid	3	2.5
390	33.6	30	16.1	26.6	19.1	2.3	91	16.9	1	mesothyrid	2.5	1
407	47.8	42.8		37.1	26.1	3	112	26	2.1	mesothyrid	2	2
656	28.4	25		24.6	15.3	2.8	106	19.2	1.7	submesothyrid	3	2
659	32.1	28.8	16.1	27.3	17.6	2.1	111	18	1.4	mesothyrid	2	1
669	29.1	25.4	13.8	25.8	15.1	2.3	105	19.4	1.6	mesothyrid	2.5	2
673	38.6	34.7	22.4	32.9	20	2.3	103	23.7	2.3	mesothyrid	2	3
721	31.4	28.3	16.2	28.9	15.4	2	117	21.4		mesothyrid	2.5	1
722	41.2	36.6	23.2	31.5	22.2	3.1	98	24.6	1.6	mesothyrid	2.5	3
724	34.7	31	16.4	30.2	17.1	2.3	113	20.5	*1.3*	mesothyrid	2	2.5
727	35	31	18.7	29.6	17.3	2.3	105	19		mesothyrid	2.5	2
730	30.9	27	16.2	25.5	16.9	2.1	99	18.2	1.1	mesothyrid	2	1
734	41.1	36.5	21.2	32.7	22.4	2.8	97	22.5	1.9	mesothyrid	2	2

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
735	34.9	31	17.1	27.9	19.2	2.3	98	19.4	1.5	mesothyrid	2.5	2.5
855	28.9	25.8	16	26.1	14.8	2	110	19.4	1.4	mesothyrid	3	2.5
861	32	28.8	*16.7*	31.3	16.2	2.1	123	21.8	1.4	mesothyrid	3	3.5
862	37.1	32.9	*18.1*	31.3	19.7	2.4	111	23.7	1.6	mesothyrid	2	2
863	35.7	31.7		31.2	18.7	2.3	111	23.1	1.5	mesothyrid	3	2.5
864	31.5	27.4	17.1	26	16.5	2.8	95	19.9	1.4	mesothyrid	2.5	2
865												
866	31.4	27.9	16.5	25.7	17.4	2.2	95	17.3	1.2		3	2
871	31.5	28.2	17.7	27.3	18	2	98	20		mesothrid	2	2
872	31.8	28	15.8	27.3	17.2	2.6	100	20.5	1.6	mesothrid	2.5	2
939	42.2	37.8	*22.7*	34.8	20.5	2.3	110	26.8	1.5	mesothyrid	3	2
940	34.3	30.4	19.1	28.5	18.7	2.3	111	21.4	*1.5*	mesothyrid	2	2
944	37.7	32.7	18.5	28.5	20.3	2.8	88	18.9	1.5	mesothyrid	3	0
948	39.4	34.8	21.2	33.6	21	3	101	22.5	1.6	mesothyrid	2	2
950	23.5	20.5	11.4	19.2	12.7	1.9	95	13.3	1	mesothyrid	3	1
952	24.6	21.8	11.5	21.4	13.3	1.8	103	15.2	1	mesothyrid	2	0.5
953	39.1	34.9	20.7	32	20.5	3	102	23.2	2	mesothyrid	2	2
954	41	36.8	*20.8*	33.3	22.8	3.3	97	23.9	1.8	mesothyrid	2	2
957	33.4	29.9	19.3	27.6	18.1	2.4	102	21.7	0.8	mesothyrid	3	*1*
959	49.8	45.5	*25.7*	42	26	2.5	116	27.4	2.1	mesothyrid	2	3
960	57.2	51.8	28.5	45.9	29.5	3	122	28.3	2.2	mesothyrid	3	2.5
967	48.8	43.5	25	40.2	27.1	2.2	96	25.8	1.7	mesothyrid	3	3
2242	44.6	39.3	22.8	32.7	22.5	3.2	102	23.6	1.7	mesothyrid	2	4
2244	30.6	26.9	15.5	23.8	17	2.1	95	16.9	2	mesothyrid	2.5	2
2246	44.2	38.9	21.7			3.5	101	29.8	1.9	mesothyrid	2.5	2.5
2247	42.4	37.9	*23.4*	31.5	23.4	3	104	23.1	1.8	mesothyrid	2.5	2
2248	36.7	32.7	18	31.1	19.5	2.5	103	22.1	1.4	mesothyrid	3	2

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
2249	29.6	26.1	15.4	25.7	15.4	2.1	109	18.9	1.5	mesothyrid	2.5	3
2250	37.9	33.4	*17.8*	30.7	20.7	3.3	99	22.6	2	mesothyrid	2	3
2251	34.5	30	*18.9*	28.7	19.6	2.7	101	21.9	2.3	mesothyrid	2	3
2253	36.8	32.8	19.1	31.4	20.1	2.1	97	22.1	1.7	mesothyrid	3	3.5
2254	28.8	25.1	15.8	23.2	17.1	2.1	92	15.8	1.2	mesothyrid	2.5	3
2256	42.1	37.5	20.6	35.5	21.5	2.8	101	25.9	2	mesothyrid	2.5	2
2257	39.1	34.6	*19.1*	29.5	21.8	3	106	22	1.7	mesothyrid	2	3
2264	29.1	26.5	12.3	27.1	15.5	1.8	117	18.9	*1.2*	submesothyrid	2.5	0.5
2267	41.8	36.3	*24.5*	30.9	23.7	3.2	94	23.5	2.2	mesothyrid	3	2
2309	45.6	40.1	27.5	38.2	24.3	2.3	92	*30.7*	2.2	mesothyrid	3	3.5
2310	39.2	34.9	22.6	32.2	21.3	2.3	111	24	2.1	mesothyrid	2.5	2
2313	26.4	23.2	12.2	22.3	14.1	2.1	105	17.4	1.2	submesothyrid	3	1
2315	36.5	32.8	*20.3*	29	18.2	2.5	100	21	1.5	mesothyrid	3	3.5
2316	39	34.1	22.8	31.6	22.9	2.4	93	22.1	1.9	mesothyrid	3	2.5
2317	33.4	29.3	16.9	26.7	18.5	2.8	109	28.2	1.1	mesothyrid	2.5	1
2318	36.9	32.4	19.4	31	19.7	3.1	105	23	1.8	mesothyrid	2	2.5
2320	38.7	34.1	20.8	30.6	21.1	2.9	107	22.2	1.8	mesothyrid	2	3.5
2321	30.1	26.8	15.5	25	16.7	1.9	103	16.5	1.1	mesothyrid	2.5	3
2327	34.4	30.7	18	27.8	18.1	2.5	110	20.6	1.4	mesothyrid	2	2.5
2330	37.2	32.8	19.1	32.1	20.5	2.8	118	23.2	1.5	mesothyrid	2.5	2.5
2333	32.5	28.6	17.7	26.5	17.2	2.7	100	19.1	1.1	mesothyrid	2.5	2
2334	42	37.6	22.5	35.6	22.2	2.9	113	25.9	1.7	mesothyrid	2.5	3.5
2337	36.9	32.8	22.1	31.2	19.3	2.3	100	21.9	1.5	mesothyrid	3	2
2338	44.4	39	*24.3*	36.4	23.3	3.2	99	29	2.2	mesothyrid	3	2
2343	42.8	37.6	*22.3*	33	24.7	2.8	87	23.2	2.5	mesothyrid	3	1.5
2346	48	42.5	28	38.1	27.1	3.2	105		2.1	mesothyrid	3	3.5
2347	41	36	*21.3*	33.2	21.1	3	98	23.2	1.7	mesothyrid	3	2.5

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
2348	35.6	31.4	17	25.9	21	3	89	*18.1*	1.5	mesothyrid	2	2
2349	32.2	28.7	16.2	26.5	16.7	2.7	97	19.8	1.9	mesothyrid	2	1.5
2350	29	26.1	12.8	26.7	15	1.8	116	19.4	1.3	mesothyrid	3	1
2351	28.5	25.5		24.9	15	2.2	105	17.4	1.2	mesothyrid	2	0.5
2353	33.1	28.8	16.7	24.5	16.4	2.5	106	19.1	2.1	mesothyrid	2	1
2354	37.9	33.5	20.8	28.6	21.5	2.9	93	20.7	1.9	mesothyrid	2.5	1.5
2355	34.6	30.6	18.4	29	18.2	2.4	104	20.7	1.6	mesothyrid	3	2
2357	43.8	38.2	25.5	34.7	24.7	2.9	92		2.4	mesothyrid	3	2
2359	42.2	36.9	25.2			3	97		2	mesothyrid	3	3
2362	40.8	36.8	22			2.4	102	23.3	1.8	mesothyrid	3	3

Duntroon

Italicised entries are approximate due to slight crushing of shell etc.

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
588	40.5	37.8	16.1	31.5	19.9	1.6	107	19.4	0.8	submesothyrid	3	0.5
589	33.7	31.1	15.2	29.4	17.2	1.7	121	17.8	1.1	mesothyrid	3	0.5
590	29.6	26.8	14.4	24.8	14.4	2.1	98	16.9	0.7	hypothyrid	3	1
591	31.6	28.4	15.4	25.5	15.4	1.8	103	15.7	1.1	mesothyrid	3	1.5
593	30.5	27.7	13.5	27	16.3	2	115	19	0.9	mesothyrid	3	0.5
594	30.3	28	13.1	25.3	15.6	1.3	107	16.4	0.9	mesothyrid	2.5	0
600	25.8	23.3	11.6	21.5	15	2	99	13.5	0.8	hypothyrid	3	0
602	25.7	23.1	11.5	21.8	13.1	1.9	114	15	1	mesothyrid	3	0.5
603	18	15.6	8.9	14.8	9.1	1.6	109	11.6	0.7	submesothyrid		1
604	23.6	21.4	11.2	20.2	12.1	1.1	103	12.6	1.1	mesothyrid	3	0
605	24.8	22.7	12.3	20.7	12.3	1.4	108	13.6	1.2	mesothyrid	3	2
607	23.1	21	11.2	18.9	11.1	1.2	107	12	1.1	mesothyrid	3	1
608	19.9	18.2	9.1	16.9	9.3	0.9	108	11	0.8	mesothyrid	3	0
609	20.6	18.6	9.5	16.8	10.4	1.1	106	12.4	1.3	mesothyrid	2.5	1
611	28	25.7	13.1	22.9	14.2	1.4	104	14.1		mesothyrid	3	2
612	28.7	26.1	13.4	23.9	15.2	1.4	105	17.5	1.1	mesothyrid	3	0.5

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
613	29	26.7	12	23.9	14.9	1.6	106	14.3		mesothyrid	3	0
619	13.9	12.5	6	11.4	6.2	1	104	8.7	0.5	submesothyrid	3	0.5
620	16.5	14.5	7.8	13.2	8.2	1.3	101	8.7	0.9	mesothyrid	2	2
622	14.6	13.1	6.9	12.2	7.3	1.3	95	9	0.8	submesothyrid	2	0.5
623	16.2	14.6	7.9	14.2	8.4	1.5	96	9	0.9	mesothyrid	2.5	1
624	18.1	16.4	7.7			1.2	115	11	0.8	mesothyrid	3	0
625	25.1	22.9	11	22.9	13.2	1.5	114	14.6	1	hypothyrid	3	0
626	23.4	21.5	11.9	22.3	12.5	1.4	113	13	0.8	submesothyrid	3	0.5
630	21.6	19.7	9.9	19.4	10.5	1.4	115	13.1	0.8	mesothyrid	3	1
631	18	16.2	8.2	15.7	8.5	1.3	112	11.3	0.7	submesothyrid	3	1
632	17.8	16.1	10.1	13.7	9.1	1.2	90	9.9	1	mesothyrid	2.5	0.5
634	27	24.6	14.1	20	14.6	1.6	112	11.5	0.9	mesothyrid	2.5	0
635	23.2	21.2	11.4	18.5	12.4	1.2	95	11.1	1	mesothyrid	3	0.5
636	23.2	20.9	13.4	18.5	12.9	1.6	94	12.7	0.9	submesothyrid	3	2.5
1033	24.2	22.2	12.8	20.6	14.3	1	110	13.1	0.7	submesothyrid	4	0.5
1034	26.6	24.4	11.4	23.9	12.8	1.4	109	15.6	0.9	submesothyrid	3	0.5
1035	21.9	19.3	9.6	18.5	12.2	1.6	99	12.4	1	hypothyrid	3	0
1036	25.5	23.6	11.6	20	13.8	1.2	111	12.5	0.9	mesothyrid	3	0
1037	28.3	25.5	14.9	24.5	15.6	1.5	114	16.7	0.8	hypothyrid	4.5	1
1038	25.5	22.7	11.4	23.1	14	1.8	110	14.8	0.9	submesothyrid	3	0
1039	24.1	22.1	10.5	20.4	11.2	1.5	115	12.2	0.6	submesothyrid	3	0.5
1040	33.6	30.9	14.8	29.6	16.1	1.6	116	17.5	0.6	mesothyrid	3	0.5
1041	27.4	24.6	13.1	24.9	14.2	1.7	111	16.1	1.1	submesothyrid	3	0
1042	27.6	25.1	13.2	23.7	14.8	1.9	111	17	1	mesothyrid	3	2
1043	24	21.7	11.8	19.1	13.5	1.6	107	12.3	0.7	submesothyrid	3	0
1044	29.1	26.6	13.9	25.8	16.2	1.9	120	16.1	1	mesothyrid	3	0
1045	29.2	26.4	14.3	24.8	16.2	2	107	15.2	1	submesothyrid	3	0.5
1046	29	26.6	14.8	24.4	15.8	1.5	108	15	1.1	mesothyrid	3	1
1047	23	20.6	11	18.3	12.5	1.6	95	12.1	0.6	hypothyrid	3	0.5
1048	25	22.5	13	21.2	12.7	1.4	106	14.8	0.9	mesothyrid	3	0
1049	23.6	21.1	11.5	19.1	12.1	1.6	101	13.2	0.7	submesothyrid	3	0
1050	25.2	22.8	11.5	21.4	12.5	1.7	112	14.3		hypothyrid	3	0
1051	29	26.1	15.1	22.4	15.2	2.1	99	17.2		mesothyrid	3	0.5
1052	27.2	25	12.2	24.6	11.9	1.6	114	14		submesothyrid	3	0
1053	29.3	26.9	13.8	24.8	14.7	1.7	106	15.1	1	submesothyrid	3	0

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
1054	27.5	25	12.2	23.9	15.4	2	107	14.6	0.7	submesothyrid	3	0.5
1055	31.9	29.3	15.1	28.2	16.6	2	114	17.5	0.9	submesothyrid	3	0
1056	30.9	28.4		26	16.1	1.9	112	17.3	0.8	hypothyrid	3	1
1058	25.7	23.3	12.6	22	13.2	1.6	115	14.2	1.1	mesothyrid	3	1.5
1059	30.5	27.7	14.5	26.1	15.7	2	107	16	0.7	mesothyrid	3	1

Devil's Bridge

Italicised entries are approximate due to slight crushing of shell etc.

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
1928	34.8	30.3	15.2	29.1	16.4	2.4	112	20.6	1.4	mesothyrid	3	2
1929	34.9	31.6	19.9	29.1	19	2.1	102	19.1	1.8	mesothyrid	3	2
1930	36.2	32.4	18.7	30.6	19.5	2.3	97	19	1.5	mesothyrid	3	1.5
1931	35.5	32	18.9	31.4	19.8	2.4	110	19	1.9	mesothyrid	3	1
1932	42.4	38.5	21.3	35.3	23.4	2.4	112	22.5	2.3	mesothyrid	2.5	2
1933	37.9	33.9	20.5	32.2	22.2	2.9	101	21.4	1.9	mesothyrid	3	2.5
1934	37.7	33.9	20.3	32.6	21.5	2.2	103	21.5	2.2	mesothyrid	2.5	1
1935	32.8	28.8	16.2	26.6	16.8	2.2	99	16.8	1.6	mesothyrid	3	2.5
1936	36.1	33.2	18.8	31	20.4	2.4	103	18.9	1.4	mesothyrid	3	2
1937	37.5	33.5	20.2	33.8	20.5	2.6	124	23.5	1.9	mesothyrid	2.5	2
1938	39.7	35.8	19.9	34.4	21.3	2.5	110	22.6	2.2	mesothyrid	2.5	2
1939	36.1	32.9	19.3	37.5	20.2	1.8	97	16.6	2.2	mesothyrid	2.5	2
1940	37.4	33.8	18.8	30.4	20.1	2.6	113	20.8	1.8	mesothyrid	2.5	1
1941	36.9	34.1	21.5	34.7								
1942	31.7	28.6	17.4	27.8	17.2	2.3	107	19.6	1.6	mesothyrid	3	2.5
1943	35.5	32.5	18.6	27.5	19.3	2.2	101	18.6	2.4	mesothyrid	2	2
1944	35.1	31.8	18	31.5	18.3	2.3	111	21.6	1.4	mesothyrid	2.5	2
1945	35.6	31.5	19.6	29.9	19.6	2.5	104	19.7	1.9	mesothyrid	2.5	2.5
1946	34.9	31.7	19.2	29.8	18.1	2.2	101	18.4	2	mesothyrid	3	2
1947	39.6	35.4	20.3	32.8	21	2.6	99	21.5	1.5	mesothyrid	3	1.5
1948	37	33.1	20.8	30.6	20.5	2.5	115	22.8	1.7	mesothyrid	3	2.5
1949	33.8	31.1	17	28.2	16.4	2.6	114	19.7	1.5	mesothyrid	3	2
1950	36.6	32.5	20.3	31.5	20.5	2.4	102	20.8	1.4	mesothyrid	2.5	2
1951	36.1	32.9	19.6	31.4	17.5	2.2	108	20.3	1.6	mesothyrid	2	1
1952	33.2	30.1	45.8	29.9	17.3	2	114	21.8	2.2	mesothyrid	2.5	2
1953	42.3	39.3	20.5	34.3	22.1	3	108	25.2	1.9	mesothyrid	3	2
1954	37	33.8	20.2	32.1	20.1	2.9	100	21.7	1.9	mesothyrid	2.5	2.5
1955	37.2	33.8	20.9	29.9	20.5	2.3	90	20	1.7	mesothyrid	3	0.5
1956	37.4	33.3	21.2	32.9	21.9	2.4	93	19.5	1.8	mesothyrid	2	2

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
1957	38.5	34.3	22.4	31.9	20.4	2.1	121	22.6	1.9	mesothyrid	3	2
1958	35.9	29.9	18.3	30.1	21.7	2.5	99	21.4	1.9	mesothyrid	2	2.5
1959	34.8	31.2	17.2	28.4	19.3	2.5	110	20	1.6	mesothyrid	2.5	1
1960	37.3	34.4	19.7	27.8	21.8	2.1	103	*18.7*	2	mesothyrid	2	1.5
1961	34.7	31.9	18.3	27.1	20.1	2.3	99	15.6	1.9	mesothyrid	2.5	1
1962	40.4	36.7	20.3	34.3	19.6	2.2	117	24.9	2	mesothyrid	3	2
1963	36	32.7	20.7	28.6	18.5	2.4	107	22.1	1.8	mesothyrid	2	3.5
1964	39	35	20.9	30.3	22.4	2.9	105	22	2.2	mesothyrid	2	2.5
1965	26.8	24.5	16.2	21.5	14.4	1.5	105	15.3	1.4	mesothyrid	3	1
1966	26.1	23.4	11.7	21.1	11.5	1.8	100	13.9	1.3	mesothyrid	3	0.5
1968	42	36.5	23.7	31.9								
1969	36.1	32.2	18.7	30.2	18.4	2.7	114	22.8	1.5	mesothyrid	3	2.5
1970	32.6	29.2	14.2	26.4	15.4	2.3	92	16	1.4	mesothyrid	3	1.5
1971	28.9	26.6	15	22.6	16	2.3	89	16.1	1.3	mesothyrid	3	2
1972	35.9	32.6	19	29	18.9	2.6	108	22.4	1.8	mesothyrid	2.5	2.5
1973	26.4	23.7	13.3	22.6	14.1	1.9	104	16.1	1.1	mesothyrid	2.5	0.5
1974	23.2	20.9	11.1	20.7	11.5	1.7	113	14.6	*1.6*	mesothyrid	*2*	1
1975	34.7	32	20.2	30.3	18.9	2.2	107	21	2	mesothyrid	3	2.5
1976	35.8	31.8	18.6	30.6	19.8	2.6	112	21.1	1.6	mesothyrid	2.5	
1977	36.1	32.9	19.2	29	19.3	2.3	99	20	1.7	mesothyrid	3	2.5
1978	37.4	33.6	17.8	31	18.2	2.8	107	21.1	1.7	mesothyrid	2	1.5
1979	33	30.2	16	28.6	17	2.1	103	18.5	1.3	mesothyrid	3	1.5
1980	32	29	18.8	25.5	16.4	1.8	108	18.4	1.8	mesothyrid	2.5	1.5
1981	35.1	32	18.7	30.7	19.8	2.4	107	22.9	1.8	mesothyrid	3	2.5
1982	36.4	22.9	18.9	30.4	18	2.3	104	20.9	2	mesothyrid	2.5	2.5
1983	36.9	32.9	21.5	31.9	20.8	2.2	109	22.1	1.9	mesothyrid	2.5	2
1984	40	36.4	20.4	35.8	22.7	2.6	106	23.2	1.5	mesothyrid	3	2
1985	38.7	35	20.9	32.4	20.1	2.1	94	22.8	1.8	mesothyrid	3	2
1986	39.1	35	18.5	31.7	20.7	2.9	109	23.1	2	mesothyrid	3	2
1987	32.3	28.3	18.1	25.2	17.3	2.3	95	22.2	1.6	mesothyrid	3	2
1988	40.7	37.2	23.1	31.7						mesothyrid		
1989	36.3	32.9	19	29	18	2.2	98	19.9	1.7	mesothyrid	2.5	2
1990	26.5	24.1	13.3	21.7	12.1	1.8	106	14.1	1.5	mesothyrid	2.5	1
1991	39.6	35.9	20.3	29.5	20.8	2.4	106	20.8	1.8	mesothyrid	3	2
1992	24.2	21.6	12.8	19.7	12.1	1.4	89	13.7	1.1	mesothyrid	2.5	
1993	34.5	32.3	18.2	29.8	19.9	2.3	97	18.4	1.9	mesothyrid	3	2
1996	34.5	30.7	17.1	28.6	20.9	2.5	114	19.3	1.7	mesothyrid	3	3
1997	34.1	30.6	16.5	27.1	17.3	2.4	107	20.9	1.8	mesothyrid	3	2

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
1998	31.6	27.6	14.6	26.4	14.4	2	111	18.4	1.6	mesothyrid	2.5	2
1999	33.7	29.7	18.7	29	19.7	2.7	101	22.1	2	mesothyrid	3	2
2020	30.9	27.8	17.1	25.1	15	2	100	18.2	1.4	mesothyrid	3	3
2021	36.1	32.1	19.3	30.5	19.4	2.4	112	21.5	1.3	mesothyrid	2	2.5
2022	40	36.5	19.9	29.5	20.9	2	109	19.6	2.1	mesothyrid	2.5	1
2023	29.7	27	14.6	24.3	16	1.8	100	17.1	1.5	mesothyrid	2.5	1
2024	33.1	29.2	16.9	26.4	17.5	2.9	95	20.7	1.2	mesothyrid	2	2
2025	35.2	31.2	21.4	28.5						mesothyrid		
2026	36.5	32.8	17.9	30.3	19.4	2.5	98	19.9	2	mesothyrid	2.5	2.5
2027	37.2	33.8	18.5	31.6	22	2.4	106	20.4	1.9	mesothyrid	2.5	1.5
2028	35.2	32.6	18.3	29.3	19.3	2.6	101	20.2	1.7	mesothyrid	2	1
2029	33	30.1	16.5	28.7	18.8	2.3	111	19.6	2	mesothyrid	2	2
2030	35.3	31.5	17.9	31.7	17.9	2.6	114	23.8	2.2	mesothyrid	2.5	2.5
2031	35.8	32	19.6	28.8	20.1	2.1	84	24.8	2	mesothyrid	3	2
2032	34.5	30.8	19.3	27.4	16.7	2.2	110	19.3	1.6	mesothyrid	2.5	2
2033	33.3	29.7	17.4	27.8	18.6	2.4	107	20	1.9	mesothyrid	2	2
2034	38.6	35.6	21.8	34.6	20.9	2.5	119	26.4	1.9	mesothyrid	3	2
2035	33	29.5	18.3	26.5	17.6	2.3	117	16.8	1.9	mesothyrid	2	2
2036	30.2	27.6	13.5	24.6	13.7	1.9	98	16.7	1.4	mesothyrid	2	0.5
2037	34.1	30.6	17.7	28.4	18.7	2.4	109	20.9	1.8	mesothyrid	3	1
2038	32.4	29.8	16.2	28.7	17.5	2.6	120	20.6	1.6	mesothyrid	2	1
2039	35.1	32	18.6	26.1	17.9	2.1	98	19	1.5	mesothyrid	2.5	2.5
2040	34.6	31.5	18.3	29.7	16.8	1.9	102	18.7	1.6	mesothyrid	2.5	1
2041	39.2	25.1	19.6	32.3	22	2.3	91	23.5		mesothyrid	2	2.5
2042	36.9	33.3	19.1	30.2	20.5	2.4	97	19.1	1.6	mesothyrid	3	2.5
2043	31.1	28.1	16.4	38.6	15.9	2	104	18.7	1.8	mesothyrid	3	2
2044	39.5	35	20.5	30.7	21.7	2.4	99	21.2	1.9	mesothyrid	3	3
2045	34.5	30.8	19.5	28	19	2.3	103	20.6	2.1	mesothyrid	2	2
2046	33.2	30	16.9	27.7	16.7	2	105	18.6	1.6	mesothyrid	2.5	1
2047	26.9	23.2	14.1	21.5	16	2.5	87	15	1.7	mesothyrid	2	1
2048	19.2	17.9	9.3	19.3	9.4	1.5	106	14.5	1.1	submesothyrid	3	
2049	33	29.3	15.9	29.6	16.2	2.5	106	20.8	1.8	mesothyrid	2.5	0.5
2050	37.3	33.7	19.5	30	19.7	2.1	108	23.4	1.7	mesothyrid	3	0.5
2051	33.9	30.1	17.8	29.8	16.2	2.3	114	22.5	2	mesothyrid	3	2
2053	34.1	31	16.9	29.2	19.2	2	108	18.2	2.3	mesothyrid	2	1.5
2054	41.6	37.9	19.5	36	21.4	2.3	121	22.6	2	mesothyrid	2	2.5
2055	29.9	27.1	11.6	24.8	14.7	1.6	105	20.5	1.6	mesothyrid	3	2
2056	36.8	33.9	19.6	29.6	20	2.6	107	20.9	1.3	mesothyrid	3	2
2057	24.3	21.6	11	20.4	10.4	1.5	113	14.1	1.6	mesothyrid	2.5	1

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
2058	41.7	37.3	20.6	35.7	22.2	2.5	110	25.5	2.3	mesothyrid	3	1.5
2059	41.8	37.5	23.9	36.8	23	2.3	110	27.8	1.8	mesothyrid	3	2.5
2060	30.6	27.6	15.9	26.2	15.2	2.2	117	17.6	1.4	mesothyrid	2.5	2
2061	32.9	30.1	15.5	28.1	17.1	2.1	104	17.4	1.5	mesothyrid	2	0.5
2063	24.8	21.9	12.5	31.3	13.7	2.1	94	17.1	1.4	mesothyrid	2.5	
2064	26	23.4	12.4	23.2	11.9	2.1	115	18.4	1.5	mesothyrid	3	2
2065	29.1	26.4	13.9	25.2	14.3	2	109	18.2	1.5	mesothyrid	3	1
2066	31.9	28.5	15.8	26.8	16.7	2.1	104	19.9	1.8	mesothyrid	3	1
2067	32.1	28.8	16.8	29.6	18.2	2.6	109	22.1	1.7	mesothyrid	2	3
2068	27.5	24.6	20.4	35.5	14.4	2	101	18.5	1.5	mesothyrid	2	1
2069	32.3	28.9	17.6	26.9	14.3	2	109	21.8	2	mesothyrid	3	2.5
2070	26.1	23.5	12	22.3	13	1.6	105	14.2	1.3	mesothyrid	2.5	0.5
2071	33.3	29.2	17.7	27.6	17.8	2.3	88	21.2	1.7	mesothyrid	3	2
2072	33.8	30.4	19.3	27.6	17.2	2.1	114	18.1	1.8	mesothyrid	3	2.5
2073	33.3	29.7	17.8	27.3	17.1	2.1	109	19.8	1.3	mesothyrid	2.5	2

Kokoamu Bluff

Italicised entries are approximate due to slight crushing of shell etc.

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
7116	19.2	17.6	8.6	17.1	10.1	1.4	110	11.2	0.8	submesothyrid	3	0.5
7117	19.1	17.3	10.1	15.6	10	1.3	114	10.2	1	submesothyrid	3	0
7118	24.7	22.6	11	21.1	13.4	1.4	110	14.1	1	mesothyrid	2.5	1
7119	22.3	20.4	11	17.8	11.8	1.3	104	*13.7*	1	mesothyrid	2	1
7120	21	19.1	9	18	11	1.1	110	11	1	mesothyrid	2.5	0
7121	19.4	17.5	9.5	16.6	9.5	1.1	103	10.8	1	mesothyrid	2.5	0.5
7122	21.6	20	10.9	18.9	10.4	1.1	111	12.7	0.8	mesothyrid	2.5	0
7123	22.6	20.7	10.7	19.2	11	1.2	109	11.6	0.9	mesothyrid	3	0
7124	18.5	16.7	18.2	16.4	9.6	1.2	102	10.3	0.9	mesothyrid	2.5	0.5
7125	22.3	20	10.2	18	11.7	2	106	13.2	1	mesothyrid	3	1
7126	19.7	18	8.1	16.6	9.4	1.2	104	10.8				0.5
7127	18.7	16.7	9.7	16.4	9.8	1.3	100	11.7	0.8	submesothyrid	3	0.5
7129	26.6	24.5	11.6	22.2	13.2	1.5	103	14.2	0.6	submesothyrid	3	0
7130	25.3	22.1	14.1	20.4	12.9	1.6	107	15	0.8	mesothyrid	3	0.5
7131	25.2	23	12.3	21.1	13.9	1.6	90	13.6	0.8	mesothyrid	3	0.5
7132	27.8	25.1	14.1	23.8	14.5	1.9	117	15.9	0.8	submesothyrid	3	0
7134	22	19.8	12.1	20	11.2	1.4	114	13.5	0.9	mesothyrid	3	0.5
7135	24.5	22.1	10.6	20.8	13	2	114	14.8	0.9	submesothyrid	3	0.5

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
7136	23.9	21.6	11.1	20	12	1.6	107	12.7	0.7	submesothyrid	3	0
7137	20.3	18.3	9.5	18.1	11.2	1.3	99	11.8	1	submesothyrid	3	0
7138	22.4	20.4	10.3	17.1	12	1.5	113	12.4	1.2	mesothyrid	2.5	0
7139	23.2	21.1	10.7	20.8	12.1	1.6	101	12	1.4	mesothyrid	2	0
7140	24.2	21.8	11.3	19.6	13.2	1.6	96	13.7	1	mesothyrid	3	0
7141	23.4	21.1	11.9	20.3	13.5	1.4	98	11.9	1.1	mesothyrid	3	0.5
7142	24.2	21.9	10.6	20.1	12.1	1.7	97	11.6	1.1	submesothyrid	3	0
7144	22.2	20	11.1	18.7	10.3	1.4	115	11.9	0.8	mesothyrid	3	1
7145	23.8	21.3	11.2	20.9	12.1	1.8	106	12.8	1.2	hypothyrid	3	0.5
7146	24.4	22.5	10.7	20	12.6	1.4	108	12.8				0
7147	23.3	21.1	10.6	18.7	13	1.4	97	14.1	0.8	mesothyrid	3	0
7148	23.4	21.2	11.5	19.8	11.9	1.5	107	13.2	0.9	mesothyrid	3	0.5
7149	23.8	21.7	10.1	20.4	12.5	1.6	115	12	1.1	mesothyrid	3	0
7150	21.4	19.3	10.3	18.3	11.3	1.5	97	13.1	0.8	mesothyrid	3	0
7151	20.5	18.6	9.2	17.8	11.3	1.3	98	12	1.1	mesothyrid	2.5	0
7152	21.1	19.1	10	17.7	11.6	1.4	100	11.4	0.7	mesothyrid	3	0.5
7153	20	18.1	8.7	17.2	9.5	1.3	110	12.1	1	mesothyrid	2.5	1
7154	20.9	19	10.3	19	10.6	1.3	109	12.4	1	mesothyrid	2	1
7155	23.3	21.1	12.1	18.2	12.2	1.5	103	14.5	0.5	mesothyrid	3	1
7156	20.7	18.4	9.7	17.5	11.3	1.6	94	11.8	1.2	mesothyrid	3	1
7157	22.8	20.6	10.8	20.7	11.8	1.6	111	13.5	0.8	mesothyrid	2.5	0
7158	21.8	19.7	10.7	18.7	11.7	1.5	112	14.2	1	mesothyrid	2.5	0.5
7159	20.1	17.6	11.1	17	10.4	1.6	107	13	0.7	mesothyrid	3	1
7160	18.2	16.5	8.2	14.9	9	1.1	104	10.8	0.8	mesothyrid	2.5	0
7161	18.9	17	7.1	16.4	9.6	1.6	96	10.8	0.7	hypothyrid	3	0
7162	17.7	16	8.4	14.8	10	1.3	99	10.1	0.7	mesothyrid	3	0.5
7163	16	14.2	7.3	14.2	8.1	1.2	101	8.7	0.6	mesothyrid	3	0
7164	17.9	15.9	7.6	15.4	9.4	1.7	100	10.5	0.8	submesothyrid	3	0.5
7165	15.1	13.3	7.2	13	7.8	1.1	97	8.5	0.9	mesothyrid	3	0

Clifden Quarry

Italicised entries are approximate due to slight crushing of shell etc.

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26270	62.8	56.2	29.9	49.2	33.5	3.2	115	33.4		mesothyrid	3	3
26271	54.1	48.8	26.5	42.1	30.3	3.7	104	26.8		mesothyrid	3	3.5
26272	48.7	43.8	21.3	38.9	24.1	3.1	107	24.8		mesothyrid	2.5	1
26273	53.5	48.7	20.2	41.4	27.7	3.7	105	27.7		mesothyrid	3	2
26274	50	44.9	*19.1*	43.1	27.1	3.6	103	27.8		mesothyrid	2.5	2

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26280	43.1	38.8	22.4	32.7	23.1	3.1	90	21.8	2.1	mesothyrid	2	2
26281	40.4	36.4	21.2	32.3	22.2	2.9	102	20.1		mesothyrid	3	3
26282	52.5	47.3	23.8	41	28.4	3.2	101	28.9	2	mesothyrid	2	3.5
26285	48.1	43	25.4	39.5	28.9	3.4	96	28.6	2.4	mesothyrid	2	3
26286	47.5	42.4	23.4	39.6	25.5	2.9	104	29.4		mesothyrid	3	3
26290	47.4	42.5	26			3.3	108	26.9		mesothyrid	3	3.5
26291	47.3	42.1	24.1	32.7	26	3.4	104	22.4		mesothyrid	2.5	3.5
26292	47.7	42.3	25	37.6	28.2	2.9	96	26.1		mesothyrid	3	3
26293	44.4	39.4	23.1	34.4	22.4	3.3	107	26.4		mesothyrid	2	2.5
26294	*38*	*35*	18.8	35.1	19.6	2.5	115	29.1	1.3	mesothyrid	2	1.5
26295	44.7	39.6	22.3	37.8	23.2	3.2	116	28.9	1.8	mesothyrid	3	2.5
26296				38.7				27.5				4
26297	45.1	39.8	22.2	37	24.6	3.3	100	24.8		mesothyrid	3	2
26298	*44*	40.2	24.2	34.5	*24.7*		102	24.2				3
26299	44	39.2	22.5	33.5	21	2.9	116	26.8	2	mesothyrid	3	2
26300	44.2	39.2	24	35.9	22.8	2.5	112	25.5	2.2	mesothyrid	3	3
26301	44.4	40.1	22.8	38.9	22.4	2.8	111	28.8	1.4	mesothyrid	3	3
26302	45.9	41	20.3	37.1	23.4	3.3	112	24		mesothyrid	2	2
26303	51.2	46.4	25.6	37.5	23.6	3.1	109	27.7		mesothyrid	3	2.5
26304	44.7	39.9	23.9	36.9	23.5	3.4	105	27.4	2.2	mesothyrid	2	3
26305			25.1	36.7								3.5
26306	46.1	40.8	26.7	36.9	24.6	3.2	102	28.2	2.7	mesothyrid	2	3
26307	42.4	37.6	23.2	33	22.4	2.7	113	22.9	1.9	mesothyrid	3	2
26308	42.8	38.4	21.2	34.7	23.4	*3*	103	22.1		mesothyrid	2.5	2
26309	44.2	39.1	24.2	34.7	19.5	3.1	107	25.6		mesothyrid	2	3
26310	41.6	36.9	23.4	36.2	23.2	3.1	107	25.6	1.9	mesothyrid	3	2.5
26311	45.7	41.5	*25.1*	35.7	24.2	2.7	114	26.7		mesothyrid	3	2.5
26312	42.4	37.8	21.8	34.9	22.6	3.1	108	24.5	2.5	mesothyrid	2	2
26313												
26314	41	36.7	*20*	35.3	17.8	2.7	112	29.5		mesothyrid	2.5	2
26315	41	37.1	18.9	33.4	21.8	2.5	101	24.1	1.6	mesothyrid	2	2
26316	41.6	37.2	21.1	34.6	22.1	3.2	112	25.6	1.9	mesothyrid	2	*1.5*
26317	44	39.2	20.3	33.8	21.9	3.2	87	26.3	2	mesothyrid	2	2.5
26318	43.2	38.7	20.1	33	22.1	3.7	109	25.7		mesothyrid	1.5	2
26319	41.6	37.3	23.1	33.4	21.7	2.8	97	22.2		mesothyrid	2	3
26320	38.2	33.9	15.9	32.2	18.7	3.2	100	23.5	1.8	mesothyrid	2	1.5
26321	34.2	30.9	16.4	32.1	15.5	2.4	114	24	1.5	mesothyrid	2	1.5
26322												

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26323	32.4	29.1	17.1	30	16.5	2.3	108	22.5		mesothyrid	2.5	3

Deborah

Italicised entries are approximate due to slight crushing of shell etc.

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26818	40	36	22.2	34.8	19	1.5	115	23.1	1.6	mesothyrid	3	2.5
26819	39.5	35.7	20.6	34.3	18.5	2	98	21.8	1.7	mesothyrid	2.5	2
26820	38.3	34.1	18.7	29.6	16					mesothyrid		
26821	38	34.1	20.5	30.7	16.5	2.9	109	24.1	1.5	mesothyrid	2.5	2.5
26822	33.7	30.2	17.7	27.8	14.5	1.6	109	20	1.6	mesothyrid	2.5	2
26823	44.8	40.6	24.2	38.5	22	1.9	111	22.4	1.8	mesothyrid	3	2
26824	40.5	36.6	21.4	35.1	18.5	*1.9*	118	*22.6*	1.6	mesothyrid	3	2.5
26825	44.1	40.5	21.4	38.5	21.5	1	112	22.7	2	mesothyrid	2.5	2
26826	36	32.7	20.4	29.7	16.5	1	108	18.3	1.4	mesothyrid	2.5	3
26827	41.3	37.7	23	36.4	20	1.6	118	23.1	2.1	mesothyrid	3	2
26828	37.3	33.7	20.8	29.6	18.5	1.3	103	18.6		mesothyrid	2.5	1
26829	35.9	32.3	17.2	28.7	18	1.8	103	17.5	1.6	mesothyrid	2.5	1
26830	32.4	29.3	17.6	26.7	15	1.5	99	17	1.6	mesothyrid	3	2
26831	34.7	31.6	18.9	30	17.5	1	113	19.4	1.5	mesothyrid	3	2
26832	36.9	32.9	20.6	31	18	1.8	109	21.9	2	mesothyrid	3	1
26833	33.6	30	18.8	26.9	16.5	1.2	109	18.3	1.6	mesothyrid	3	1.5
26834	31.4	27.9	15.3	26	14.5	1.7	105	16.6	1.7	mesothyrid	2.5	0.5
26835	32	28.3	17	25.8	15.5	1.9	108	17.9	1.6	mesothyrid	2.5	2.5
26836	35.4	31.4	19.7	28.7	16	1.4	108	19.8	1.8	mesothyrid	2.5	2.5
26837	32.9	29.3	15.8	25.3	14.5	1.1	104	18	2	mesothyrid	2.5	2.5
26838	29.3	25.7	16	22.8	12	0.9	96	16.7	1.7	mesothyrid	3	2.5
26839	27.7	24	12.2	19.9	16	1.7	97	15	2	mesothyrid	2.5	3.5
26840	25.8	22.7	13.8	19.4	16	1.2	92	13.9	2.5	mesothyrid	2	2
26841	38.3	34.5	20.7	33.3	17.5	1.9	112	24.3	1.7	mesothyrid	2.5	2
26842	43.3	39.5	23.1	34.6	22	2	114	22.6	1.6	mesothyrid	3	2
26843	41	37.2	21.4	36.9	20	1.8	117	23.4	2.8	mesothyrid	2.5	1.5
26844	38.7	34.7	19.7	30.2	19	2.2	104	19.7	1.9	mesothyrid	2.5	1
26845	36	31.2	21	29.4	17.5	2	112	21.5	1.8	mesothyrid	2.5	1.5
26846	33.6	30.3	16.8	28.1	13.5	2	103	18.5	2.1	mesothyrid	2.5	1
26847	35.4	31.5	19.4	27.2	18	2.6	98	19.8	1.7	mesothyrid	3	1.5
26848	38.2	34	18.3	33.4	16.5	2.5	113	*25*	2.3	mesothyrid	3	1
26849	43.9	38.9	21.9	35.9	18.5	3	116	*27*	1.7	mesothyrid	3	2
26850	37.7	33.6	19.3	31.8	18	2.6	110	21.6	1.5	mesothyrid	2.5	1.5
26851	35	30.8	18.7	28.7	14	2.7	106	23.3	2.1	mesothyrid	2	2

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26852	31.9	27.9	18.5	24.8	15	2.7	113	17.7	1.7	mesothyrid	3	3
26853	34	31.1	18.7	28.6	15.5	2.5	109	20.7	1.4	mesothyrid	2.5	2.5
26854	37.5	34.1	16.6	32.9	15	2.4	110	23.8	1.7	mesothyrid	2.5	2
26855	33.1	29.3	16.4	29.7	15	2.8	120	22.6	2	mesothyrid	2.5	2
26856	30.1	27.1	16.7	22.3	15.5	1.8	110	16.2	1.6	mesothyrid	2.5	1.5
26857	36.8	33.7	19	30.8	18	2.1	109	20.5	1.6	mesothyrid	3	2
26858	36.7	32.7	20.9	29.3	17.5	2.3	98	20.2	2	mesothyrid	3	2.5
26859	35.6	32	17.9	29.5	16	1.9	107	18.5	1.7	mesothyrid	2.5	2
26860	41.7	38	22.1	34.5	18	2.8	113	23.8	2.3	mesothyrid	2.5	2.5
26861	38.3	35	22.9	30.6	19	1.9	107	20.7	1.3	mesothyrid	3	2.5
26862	40	35.5	21.1	32.3	19							
26863	36.8	33.1	18.5	31.9	15.5	2	117	25.2	1.5	mesothyrid	3	2
26864	31.4	28.3	14.5	24	14.5	1.9	107	17.4	1.8	mesothyrid	3	2
26865	29.4	25.7	14.2	24.3	12	2.2	104	18.5	1.3	mesothyrid	3	2
26866	35.9	32.2	16.8	30.2	16	2.4	111	22.5	1.5	mesothyrid	2.5	2
26867	43.2	38.8	21.6	33.9	20	3	103	24.4	2	mesothyrid	2.5	2.5
26868	29	26.2	12.8	23.8	11.5	1.6	105	16.3	1.5	mesothyrid	2.5	2
26869	29.4	24.5	14	26.3	11.5	2	113	20.8	1.8	mesothyrid	2.5	2
26870	33	29.5	16.4	27.3	15	2	106	19.4	1.7	mesothyrid	3	1
26871	29.9	25.3	15.2	23	13.5	2	95	17	2.1	mesothyrid	2.5	2
26872	32.2	28.7	17	25.7	15	2.3	91	19.1	1.5	mesothyrid	2.5	1.5
26873	44.4	41.1	24.2	34.9	21	1.9	108	26.4	2	mesothyrid	3	3
26874	38	34.5	29.2	32.6	17.5	2.3	104	23.3	1.8	mesothyrid	2.5	1
26875	29.2	25.2	19.8	21.4	17	2	87	15.4	1.9	mesothyrid	3	3
26876	28.1	26.3	14	24.3	12.5	1.7	109	17.5	1.6	mesothyrid	2.5	1.5
26877	27.5	24.8	12	24.9	12	1.9	111	17.8	1.4	mesothyrid	3	0.5
26878	34.7	31	18.4	31.1	15	2.2	107	20.5	1.9	mesothyrid	3	1.5
26879	33	30.3	14.9	28.4	14.5	1.9	112	19	1.6	mesothyrid	2.5	1
26880	34.2	31.3	17.4	29.8	14.5	1.9	110	18.4	2.1	mesothyrid	2.5	0.5
26881	39.9	36.1	22.5	32.5	20	1.9	98	21.2	1.7	mesothyrid	2.5	2
26882	32.3	29.2	17.5	28.1	13	1.7	112	20.8	1.3	mesothyrid	2.5	1
26883	35.8	31.4	20.5	30	15	2.3	107	24.7	2.1	mesothyrid	3	1.5
26884	41.4	35.9	21.3	30.2	20.5	3	104	23.6	1.7	mesothyrid	3	2
26885	35.3	32.5	19.2	29.3	17	2.1	103	23.1	2.1	mesothyrid	2.5	2
26886	33.7	30.4	16.2	28.7	16	2.1	108	19.9	1.7	mesothyrid	2.5	1
26887	35.8	32.3	19.1	29.1	15	2.2	114	21.9	1.9	mesothyrid	2.5	2.5
26888	40.3	36.4	22.8	33.7	17.5	1.6	101	22.3	2.1	mesothyrid	3	2
26889	31.8	28.3	16.5	28.4	15	1.9	109	21.7	1.9	mesothyrid	2.5	1.5
26890	37.2	33.4	18	31.9	15	2.3	116	25.8	1.8	mesothyrid	2.5	2
26891	29	26.5	12.6	26.2	12							

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26892	34.3	30.4	18.6	28.1	15.5	1.9	99	19.9	1.6	mesothyrid	3	2
26893	37.8	34.2	22.8	32.7	19	1.7	96	22	2.1	mesothyrid	2.5	1.5
26894	38.3	34	20.3	31.5	19	1.9	102	23.4	1.8	mesothyrid	3	1.5
26895	38.2	34.8	20.5	33.8	17	1.9	121	21.6	1.9	mesothyrid	2.5	2
26896	41.6	38.3	21.8	34.8	21	1.9	115	27.9	1.9	mesothyrid	2.5	1
26897	37.7	34.5	20.3	31.4	18	2	112	21.5	2	mesothyrid	2.5	1.5
26898	39.4	35.6	31.7	33.2	16	1.9	108	23.8	1.7	mesothyrid	3	2
26899	39.8	35.1	21.9	34.6	20.5	2.3	109	23.7	2.4	mesothyrid	3	2.5
26900	39.1	35.4	21.2	33.7	18	2.3	119	24.2	1.8	mesothyrid	3	2
26901	40.8	37.4	20.7	35.8	19	2.3	121	25.1	2	mesothyrid	2.5	2
26902	36	32.3	19.1	31.3	17	2	115	22.8	1.7	mesothyrid	2.5	1.5
26903	33.5	30.1	17.1	27.8	14	1.9	107	16.9	1.2	mesothyrid	3	1.5
26904	38.3	34.3	18.4	32	18	1.9	113	21.9	1.8	mesothyrid	3	2
26905	38.2	34.8	19.1	32.6	16	2	116	21.8	1.7	mesothyrid	3	2.5
26906	41.4	37.2	21.6	33.1	18	2.5	120	25.5	2.1	mesothyrid	2.5	2
26907	32.1	28.4	17.5	26.4	15	2.1	107	17.5	2	mesothyrid	2.5	1.5
26908	37.9	34.8	18.9	32.8	17	2.1	123	23.5	2	mesothyrid	3	2
26909	39.5	35.8	21.3	31.9	19	1.9	113	28.1	2.1	mesothyrid	3	2
26910	37.7	33.6	20.2	28.7	18.5	2.3	93	20.9	2.5	mesothyrid	3	2
26911	38.2	33.7	21.8	32	18.5	2.2	107	21.9	2.6	mesothyrid	3	1
26912	34.1	31.4	17.9	31.1	15.5	1.6	112	19.3	1.6	mesothyrid	3	1.5
26913	40.8	37	19.8	31.8	18.5	2.4	107	21.3	2.3	mesothyrid	2.5	1.5
26914	48.7	44.3	20.5	42.5	22	2.6	121	26.1	2.2	mesothyrid	2.5	2
26915	42.1	37.8	22.4	36.8	20.5	2.8	126	27	2.1	mesothyrid	2.5	2
26916	35.6	31.9	19.7	30.2	16.5	2.1	109	22.8	2.3	mesothyrid	2.5	1
26917	32.2	29.1	16	23.4	15.5	1.7	80	13.9	1.9	mesothyrid	3	1.5
26918	33.7	29.9	18.2	26.5	17.5	2.6	83	17.7	2.1	mesothyrid	2.5	2.5
26919	43.6	39.4	24.8	34.3	21.5	2.4	109	25.5	1.9	mesothyrid	3	2.5
26920	36.4	32.2	17.7	26.8	16.5	2.6	97	21.4	2	mesothyrid	2	1.5
26921	37.7	32.1	18.3	31	17	2.9	103	26.1	2	mesothyrid	3	2.5
26922	44.8	40.9	24.7	33.3	22	2.4	107	23.4	1.9	mesothyrid	3	2
26923	34.5	31.3	17.4	27.7	14	2.2	108	19.5	1.4	mesothyrid	3	2
26924	37.2	33.6	17.9	31.4	17	2.6	107	24.9	1.7	mesothyrid	3	1.5
26925	37.8	34.4	19.8	33.5	17	1.9	109	22	1.8	mesothyrid	2.5	2
26926	35.9	32.7	18.7	31.4	17	2.2	110	22.9	2	mesothyrid	2.5	2
26927	37.7	34.2	19.1	32.1	19.5	1.7	105	19.2	1.8	mesothyrid	3	1.5
26928	31.1	27.9	17.2	26	13	2	102	17.9	1.7	mesothyrid	3	2
26929	34.4	30.4	16.9	28.2	15							
26930	41.4	37.9	21.6	33.7	20	2	114	20.9	2	mesothyrid	3	1
26931	34.2	31.7	16.9	29.4	16.5	2.2	107	20.4	1.7	mesothyrid	2.5	1.5

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26932	39.6	35.9	22.4	35.3	20	2.2	118	22.6	2	mesothyrid	3	2
26933	49.4	45	21.8	39.9	24.5	2.8	102	21.9	1.9	mesothyrid	2.5	1.5
26934	38.5	34.4	20.4	28.9	20	2.3	106	19.8	1.7	mesothyrid	3	2.5
26935	38.2	34	19.3	32.9	18.5	2.9	109	23.3	2	mesothyrid	2.5	1
26936	42.8	38.2	20	38.9	20	3.1	115	25.2	1.9	mesothyrid	2.5	2
26937	42.5	38.2	22.8	38.3	18.5	2.2	113	24.4	2	mesothyrid	2.5	2
26938	31.2	28.2	15.6	25.3	12	2	97	19.4	1.7	mesothyrid	2.5	1.5
26939	31.3	28.3	14.8	25.3	13	1.7	101	17.2	1.6	mesothyrid	2	1.5
26940	35.4	32	18.4	29.2	15.5	1.9	102	18.6	1.5	mesothyrid	3	2
26941	43.3	40	22.3	36.9	20.5	2.1	107	23.4	1.6	mesothyrid	2.5	2
26942	39.4	35.9	21.7	32.6	18.5	2	113	20.8	1.7	mesothyrid	3	2.5
26943	39	35.4	21.4	34	16.5	2.3	124	23.7	1.8	mesothyrid	2.5	2
26944	37.3	33.9	19.1	31.6	16	1.7	106	23.1	1.9	mesothyrid	2.5	1.5
26945	36.4	33.2	18.4	32.1	15	2	121	22.2	1.5	mesothyrid	3	2.5
26946	38.6	35.4	18.8	31.9	17	2.2	112	19.3	1.6	mesothyrid	2.5	1
26947	37.8	34	19.6	30	19	2.6	103	20.5	1.5	mesothyrid	2.5	2
26948	38.9	35.6	20.2	32.9	22	2.2	110	24.1	1.7	mesothyrid	2.5	1
26952	41.5	37	23.4	35.1	26.2	2.3	105	24.9	2.5	mesothyrid	3	2.5
26953	37.8	35.1	22.1	30.5	20.5	1.8	108	21.7	1.8	mesothyrid	2.5	2.5
26954	34.5	31.2	18.4	30.4	19.1	2.3	97	20	1.8	mesothyrid	2.5	1.5
26955	41	37.7	21.1	36.8	21.6	2.4	115	23.3	1.7	mesothyrid	2.5	2
26956	39	35.1	19.7	36.4	21.9	2.8	124	26.6	2.1	mesothyrid	2.5	2.5
26957	36.6	33	19.5	32.3	19.7	2.5	118	22.8	2	mesothyrid	2.5	1.5
26958	38.4	34.8	20.7	34.6	19.5	2.3	114	22.5	2	mesothyrid	3	3
26960	36.8	33	18.6	31	20.1	2.5	104	21	2.1	mesothyrid	3	2
26962	38.9	35	20.2	*32.4*	20	2.8	110	23.6	1.9	mesothyrid	2.5	2
26963	38.8	34.8	21.9	33.2	21.8	2.5	105	24.8	1.7	mesothyrid	3	2
26964	35.9	32.7	19.2	31.1	20.3	2	109	19	1.5	mesothyrid	3	2
26965	37.7	34.8	20.9	30.5	18.5	1.8	105	19.9	*1*	mesothyrid	3	1
26966	38.6	35	20.6	31.5	21.8	2.4	99	20.6	2	mesothyrid	2.5	0.5
26967	36.6	32.9	18.9	28.8	18.8	2.4	102	19.9	2.3	mesothyrid	2.5	2
26968	36.3	32.5	18.3	30.6	18.7	2.3	112	*23.1*	1.8	mesothyrid	3	2
26969	34.4	31.1	18.6	30	18.3	2	110	19.1	1.5	mesothyrid	3	2
26970	36.7	33.2	18.2	32	21.3	2.2	109	23.1		mesothyrid	2.5	1.5
26971	35.8	32.9	19	31.8	19.6	1.9	104	19	1.3	mesothyrid	3	2
26972	36.5	33.1	17.9	30.6	20.5	2.4	114	20.6	1.5	mesothyrid	3	2
26973	31.5	28.5	15.3	26.2	16.8	2.3	114	18.2	2	mesothyrid	2.5	1.5

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26974	36.6	32.9	20.8	31.9	20.6	2.4	95	19.8	1.6	mesothyrid	3	2
26975	32.5	29.6	17.6	27.9	17.9	2	107	19.6	1.9	mesothyrid	3	2
26976	32.9	29.9	17.9	27.5	18.3	1.5	95	18.1	2.2	mesothyrid	2	2
26977	35.6	32.8	18.5	28.2	22.8	2	70	14.7	2.1	mesothyrid	2	2
26978	37.8	34.1	20.6	31	21.5	2.4	107	22.7	1.8	mesothyrid	3	1.5
26980	33.6	29.8	19.1	30	19.2	2.6	107	20.3	1.9	mesothyrid	3	1
26981	33.1	29.9	19	27.4	20	2.1	104	20.8	2.1	mesothyrid	2.5	2
26982	34	30.9	16.4	29.7	20.2	2.4	108	19.6	1.7	mesothyrid	2.5	1
26983	30.9	28.4	13.9	26.5	15.9	2.2	112	17.2	1.2	mesothyrid	2.5	0.5
26984	23.5	20.9	11.6	21.6	14.5	1.8	99	15.2	1.1	mesothyrid	2.5	0.5
26985	29.1	26.2	14.9	24.2	14.4	1.9	96	16.3	1	mesothyrid		0
26987	23.5	21.4	12.9	19.1	13	1.4	91	12.7	1.3	mesothyrid	2.5	2
26988	24.7	22.5	11.7	21.4	13.5	1.7	108	14.1			2.5	1
26989	*25.8*	*22.9*	13.4	20	14	1.9	81	13.2	2.1	mesothyrid	2.5	1
26990	14.2	22	12.8	20.7	12.9	1.8	104	14.6	1.3	mesothyrid	2.5	0
26991	40.2	36.7	23.1	31	23.7	2.3	110	22.6	1.7	mesothyrid	3	2
26992	40	36.5	21.8	31.6	21.4	2.1	108	22.2	2	mesothyrid	2.5	2.5
26993	48	44.2	26	36.5	25.5	2.6	111	24.8	2.3	mesothyrid	3	1.5
26994	39.5	36.5	18.8	32	20.2	2	111	19.6	1.8	mesothyrid	2.5	2
26996	41.3	38.2	21.5	31.1	21.2	2	104	23.1	2.5	mesothyrid	2.5	0.5
26997	40.5	36.7	21.9	30.4	20.8	2.5	102	19.9	2	mesothyrid	3	2
26998	41.3	37.9	22.6	32.7	20.3	2.2	108	23.8	1.5	mesothyrid	3	3
26999	35.9	32.5	19.3	27.6	21.1	2.2	85	18.7	2.5	mesothyrid	2.5	0.5
27000	37.9	34.5	20.1	29.8	20	2.2	107	20.5	1.7	mesothyrid	2.5	2.5
27001	38.7	35.1	22.4	31.7	21.9	2	96	20	1.6	mesothyrid	3	2
27002	40.8	37.1	21.4	29.5	19.9	2.4	90	19.9	2.2	mesothyrid	3	1
27003	35.8	32.8	18.9	28.4	18.3	2	100	19.1	1.5	mesothyrid	3	1
27004	37.8	34.6	20.1	32.3	18.7	1.9	105	19.5	1.7	mesothyrid	3	2
27005	38.8	35.1	19.9	30	19.8	2.7	103	20.8	1.8	mesothyrid	3	2
27006	38	35.2	21.5	30.2	19.5	1.7	101	20.4	1.3	mesothyrid	3	1
27007	38.3	34.7	19.9	30.3	18.6	2.4	109	20.9	2.1	mesothyrid	2.5	0
27008	33.5	30.5	17.6	26.4	18.6	1.8	103	19.1	1.8	mesothyrid	3	1.5
27009	26.6	23.7	13.2	22.5	14.2	2.1	107	15.2	1.1	mesothyrid	2.5	1.5
27010	36.4	33.2	19.4	28	17.9	2.2	112	19.8	1.3	mesothyrid	3	1.5
27011	36.3	32.9	18	25.1	19	2.3	83	16.8	1.7	mesothyrid	3	1
27012	37.1	33.2	19	29.3	21.3	2.8	100	*21.4*	1.9	mesothyrid	2.5	2
27013	35.4	32.3	19.2	28.8	18.6	2.2	109	20.9	1.7	mesothyrid	3	*1*

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
27014	*28.7*	26	13.9	24.4	17	1.8	105	15.1	1.1	mesothyrid	3	1

Hutchinson's Quarry

Italicised entries are approximate due to slight crushing of shell etc.

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
27109	36.1	33	18.1	28.2	18.4	2	104	20.1	1.8	mesothyrid	3	4
27110	36.4	33.1	18.2	30.6	17.4	2.4	103	23.2	2	mesothyrid	2	4
27111	38.2	34.2	18.2	29.7	19	2.3	95	23.1	2	mesothyrid	3	4
27112	38.4	35	19.8	31.1	18	2.4	105	25.3	1.6	mesothyrid	3	4.5
27113	35.9	32	17.6	27.9	18.1	2.3	107	21.3	1.7	mesothyrid	3	2
27114	43	39.2	22	31.6	20.4	2.3	102	23.5	2.3	mesothyrid	2.5	4
27115	34.4	30.5	19.2	28.9	18	2.6	115	23	1.4	mesothyrid	3	2.5
27116	34.6	31	17	27.5	17.5	2.3	98	23.7	1.2	mesothyrid	3	3
27117						1.9	106	18.9	1.7	mesothyrid		
27118	30.8	27.9	15.7	23.2	15.7	1.7	102	15.8	1.5	mesothyrid	2.5	3
27125	31.5			27.4	16.1		109		1.7	mesothyrid		4
27126	35.3	31.8	17.2	28.4	17.8	2.6	122	23.2	1.5	mesothyrid	2.5	3
27127	38.9	35.1	22.6	35.4	18.7	2.2	111	30.4	1.5	mesothyrid	3	3
27128	39.4	35.5	21.3	32.3	19	2.6	107	25.2	1.4	mesothyrid	3	3
27129	33.5	30	16.7	24.5	18.4	2.3	99	17.3	1.9	mesothyrid	2.5	2
27131	50.6	45.7	29	40.5	26.5	3.2	*115*	32	2.5	mesothyrid	3	4.5
27132	40.5	36.9	23.4	36.7	20	2.1	114	23.3	2.2	mesothyrid	2.5	4
27133	42.6	38.6	22.6	37.3	21.2	2.4	110	27.7	2.2	mesothyrid	2.5	4
27135	39.3	35.8	19.5	31	18.3	2.4	121	24.2			2.5	4
27136	40	36.2	20.4	32.7	20.4	2.5	112	25.4	1.7	mesothyrid	3	4
27137	43.3	39.3	24.4	24.3	23.3	2.5	90	23.6	2.3	mesothyrid	2.5	3.5
27138	36.3	33.1	19.6	31.2	18.1	2	106	24.9	1.6	mesothyrid	2.5	3
27139												
27140	31.6	28.3	16	26.4	15.6	2.1	111	21.4	1.6	mesothyrid	3	4
27143	34.4	31.1	16.6	28.2	19.2	1.9	86	24.7	1.4	mesothyrid	3	4
27147	30.2	27.2	15.6	25	14.1	2	98	19.3	1.6	mesothyrid	3	3.5
27148	32.9	29.1	16	26.8	16.4	2.1	95	18.8	1.5	mesothyrid	3	4
27149	36.1	32.2	19.8	25.9	19.5	2.7	94	19.5	1.5	mesothyrid	2.5	4.5
27150	31.3	28.3	15.6	25.9	15.1	2.1	92	18.5	1.8	mesothyrid	2.5	4

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
27151	32.8	29.7	16.3	25.4	17.4	1.9	102	17.6	1.5	mesothyrid	3	4
27152	32.6	29.4	16.4	26.4	16.6	2	106	21.8	1.5	mesothyrid	3	4
27153	33.5	30.3	17.3	25.7	15.9	2	90	17.7	1.5	mesothyrid	3	3.5
27154	32.4	29.1	15.8	29.5	16	2.3	105	*20.8*	1.4	submesothyrid	3	2
27155	30.1	27.3	13.7	24.9	14.8	1.9	100	20	1.5	mesothyrid	2.5	2
27157	30.3	*27.6*	13.3	25.1	15.1	1.8	103	17.6	1.5	mesothyrid	3	3.5
27158	*29.9*	*26.8*	15.4	23.5	16.1	1.8	90	15.3	1.4	mesothyrid	3	3
27159	27.6	24.8	13.2	23.4	12	1.9	107	18.2	1.8	mesothyrid	2	1
27161						1.3	107	12.8	1	mesothyrid	*2*	
27162	24.1	22	11.1	22.1	10.8	1.4	102	14.7	1.3	mesothyrid	2.5	1
27163												
27164	44.4	40.9	23	36.9	20.7	2.2	116	*31.5*	1.3	mesothyrid	3	1
27298	43.1	39.7		33.1	22	2.4	106	23.7	2	mesothyrid	2.5	4
27299	38.4	35	21.1	32.6	19	2.6	102	21.1	1.7	mesothyrid	3	4
27300						2.5	113	*26.1*	1.5	mesothyrid	3	
27301	42.7	39	*22.1*	35.9	22.4	2.6	116	26.6	2.2	mesothyrid	2	4
27302				32.3	18.3	1.8	108	24.8	1.7	mesothyrid	3.5	
27304	33.3	30.2	18.3	30.1	15.2	2.1	110	21.3	1.7	mesothyrid	3	3
27307	39.2	35.3	20.2	29	22	2.5	92	*22.3*	1.2	mesothyrid	3	*2.5*
27308	39.3	35.6	20.2	31.3	20.1	2.2	99	21.5		mesothyrid	2.5	3.5
27309	39.1	*35.5*	20.1	28	19.6	2.5	96	22.7	2	mesothyrid	2.5	4
27310	38.4	34.8		33	21.4	2.2	112	22.7	1.8	mesothyrid	3	4
27311	35.6	31.9		29.6	17.4	2.5	114	22.8	2	mesothyrid	3	3.5
27312	34.8	31	19.6	26.5	18	2.2	101	21.4	1.5	mesothyrid	3	4
27313	*33.7*	*30.1*	17.6	27.9	17.5	2.4	102	22.5	1.6	mesothyrid	3	4
27314	34	30.7	17.9	27.3	17.3	2	105	21.4	1.3	mesothyrid	3	2.5
27315	36	32.5	18.6	29.1	17.5	2.1	104	21.2	1	submesothyrid	3.5	2.5
27319	36.9	33.2	17.1	32.5	18.2	2.6	106	24.1	1.1	mesothyrid	3	2
27320	37.3	33.6	20.2	29.3	16.6	2.2	109	22.6	1.4	mesothyrid	3	*4*
27321	34.8	31.1	*17.9*	28.5	18.6	2.4	95	20.1	1.4	mesothyrid	3	3
27323	36.2	32.6	18.7	29.6	17.1	2.2	100	22.5	1.5	mesothyrid	3.5	3
27324	34.6	31.4	16.6	30.7	17.8	2.2	104	20.8	1.3	mesothyrid	3	4
27325	32.6	29.5	16.5	25.7	16.7	1.7	91	17.8	1.3	mesothyrid	3	3

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
27326												
27327	32.1	28	18.2	28.5	17.4	2.3	104	21.4	1.9	mesothyrid	3	
27329			19.1	29.4	17.4	2.3	100	23.3	1.9	mesothyrid	2.5	
27331	33.4	29.7	17.3	26.1	16.8	2.1	105	17.6	1.4	mesothyrid	3	4
27333	35	31	20.3	27.3	19.4	2.3	99	22.2	1.6	mesothyrid	3	4
27334	34.4	31.1	16.6	25.6	17.5	2.4	96	19.8	1.6	mesothyrid	2.5	3.5
27335	*34.7*	32	19.5	29.8	*15.7*	2.6				mesothyrid	*3*	4
27338	33.8	30.1		25.1	17.4	2.6	95	19.7	2.2	mesothyrid	2	4
27340	*34.9*	*31.1*	19	27	19.5	2	103	19.1	1.9	mesothyrid	2.5	0
27341				27.7	15.2	1.7	108	19.5	1.4	mesothyrid	3	
27343	29.9	26.7	15	24	16	1.9	98	15.3	1.7	mesothyrid	3	3.5
27344	30.3	27.3	14.1	27	14.5	1.5	100	18.1	1.5	mesothyrid	3	2.5
27345	29.2	26.4	15.3	25	15.1	1.4	85	16.2	1.5	mesothyrid	3.5	3
27348	*30.1*	*26.9*	15.1	28.3	13.4	1.9	112	20.2	1.3	mesothyrid	3	0.5
27349	31.3	28.2	15.7	26.8	15.3	2	104	20.4	1.4	mesothyrid	2.5	0
27350	31.1	28.1	13.6	25.3	15.1	2.3	100	15.9	1.3	mesothyrid	3	2
27351	30	27	14.5	24.1	16.9	2	97	17.7	1.6	mesothyrid	2.5	4
27353	32	28.6	15.8	24.6	17.7	2.1	112	17.1	1.7	mesothyrid	2.5	3
27355	30.5	27.5	16.9	24.9	15.2	1.9	86	17.2	1.8	mesothyrid	3	4
27356	28.2	25.5	14.2	23.1	13.5	1.5	110	16.8	1.5	mesothyrid	2.5	2.5
27359	28.6	25.1	14.9	22	13.8	2.2	92	17.6	1.6	mesothyrid	3	4.5

All Day Bay

Italicised entries are approximate due to slight crushing of shell etc.

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26720	43.5	39.8	18.7	36.5	21.4	2.3	110	19.4	2	mesothyrid	2.5	2.5
26721	36.2	33.1	16.6	31.4	20.9	2	102	17.4	1.8	mesothyrid	3	*2*
26722	40	*36*	16.9	36.1	20.6	*1.9*	116	23.1	1.8	mesothyrid	3	2
26723	41.6	38.2	21.4	34.4	21.4	2	112	21.9	2	mesothyrid	3	3
26724	*36.7*	*33.6*	16	31.8	19.5	2	106	17.5	1.4	mesothyrid	3	2

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26725	38	34.6	19.4	31.1	18.1	2.4	105	19.6	1.8	mesothyrid	3	2
26726	35.9	32.6	14.6	31.5	18.4	2.1	110	17.5	1.7	mesothyrid	3	2.5
26727	33.2	29.4	14	28.4	16.6	2.9	107	17.6	1.9	mesothyrid	3	2
26728	34.8	31.5	16.9	28.5	17.1	2.4	100	15.3	1.6	mesothyrid	3	3
26729	*40.4*	*36.6*	18	34.2	21	2.9	110	21.4	1.7	mesothyrid	2	
26730	37.2	34	19.4	30.4	18.2	2.4	108	19	1	mesothyrid	3	4
26731	36.6	33.5	14.3	32.6	18.7	2.1	120	18		mesothyrid	3	2.5
26732	35.4	31.9	14.4	28.3	17.5	2.9	104	16.8	1.4	mesothyrid	3	0
26733	36	32.1	17.4	28.6	19.3	2.8	101	18.1		mesothyrid		2
26734	35.7	32.2	14.3	30.9	17.5	2.3	107	19.3	1.9	mesothyrid	3	1
26735	37.8	34	16.8	32.5	17.9	2.7	110	19.7	1.5	mesothyrid	3	1
26739						2.5	108	18.1	1.7	mesothyrid	2	
26740	38	34.3	14.1	34.3	18.9	2.7	107	20.8	2.1	mesothyrid	2	2
26741	31.2	29.1	11.4	28.2	17	1.6	107	13.2	1.5	mesothyrid	2	1
26742	42.3	38.7	17.2	36.8	20	2.2	112	22.3	2.2	mesothyrid	2.5	1.5
26743	36.4	33.5	14.4	32	18.2	2.1	108	18.4	1.8	mesothyrid	2	2.5
26744			*14*	31.6	17.2	2.1	111	20	1.6	mesothyrid	3	
26745	*33.6*	*30.6*	15	31.1	18.3	2	102	18.5	1.7	mesothyrid	2.5	2
26746	33.3	30	14.6	30.7	17.3	2.4	110	19.4	1.6	mesothyrid	3	0.5
26747	31.7	28.5	12.5	26.5	16.3	2.2	117	17.3	1.7	mesothyrid	2	1
26748	32.6	28.6		29	17.3	2.5	99	16.2	1.8	mesothyrid	3	1.5
26749	30.9	27.8	13	27.2	16	2.4	105	15	1.9	mesothyrid	3	0.5
26750	34.1	30.7	14.1	30.1	16.8	2.3	106	17.5	1.6	mesothyrid	3	2
26752	39.2	35.2	16.3	34	21.4	2.6	112	23.6	2	mesothyrid	2.5	1
26753	27.9	25.1	14.1	27	13.7	2	121	17.7	1.3	mesothryid	3	1.5
26754	36.5	32.6	15.5	30.1	18.8	2.4	104	20.8	1.7	mesothyrid	3	2.5
26755	35.5	31.8	13.2	29.5	19.4	3	96	18.7	1.6	permesothyrid	2	2.5
26756	37.3	33.8	17.6	31.4	20.6	2.1	110	*19.2*	2.7	mesothyrid	2	2
26757			19	32	17.7	2.3	109	20.4	1.6	mesothyrid	2.5	
26758	34	31.3	13			1.8	116	16.9	1.6	mesothyrid	2.5	0.5
26759			11.4			2.4	111		1.4	mesothyrid	2.5	
26760	30.2	27.4	11.2	25.5	14.2	2.3	109	15.1	1.7	mesothyrid	2.5	1.5
26761	28.2	25.6	10.9	26.6	15	1.4	119	15	1.7	mesothyrid	2.5	1
26763	47.4	42.9	20.5	40.2	25.5	2.8	106	23.7	1.6	mesothyrid	3	1
26764	40.4	36.5	18.5	34.7	20.9	2.4	104	21.1	1.7	mesothyrid	2.5	1
26765	41.4	38	15.7	36.3	20.6	2.6	111	21.8	1.7	mesothyrid	3	0.5
26766	44.3	40.4	17.1	38.7	22.6	2.8	110	22.6	2	mesothyrid	2	3

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26767	39.6	35.5	19.2	32.3	19	2.8	104	21.2		mesothyrid	3	4
26768	36.8		13.7	34.8	19	2.3	118	22.7	2	mesothyrid	2	0.5
26769	35.8	31.7	16	33	19.3	3.1	102	19.7	1.6	mesothyrid	2.5	2
26770	35.6	32.3	*16.8*	31.3	20.3	2.4	100	19.2	1.3	mesothyrid	2.5	2
26771	35.5	32.1	16.1	32.6	17	2.8	107	19.3	2.1	mesothyrid	2	2.5
26772	32.2	29.1	12.3	29.7	14.7	2.1	112	18.1	1.5	mesothyrid	3	0.5
26773	36	33	14.3	31.6	18.2	2.2	115	19.4	1.9	mesothyrid	2	2
26774	32	28.2	*16.2*	29.1	14.5	2.4	121	20.4	1.7	mesothyrid	2	3
26775	*36*	*32.6*	14.1	30.4	20.4	2.3	106	19	1.5	mesothyrid	2.5	0.5
26776	35.9	32.1	15	29.6	17.2	2.8	103	19.4	1.5	mesothyrid	2.5	3.5
26777	34.2	31.2	14.6	27.2	18.7	2.1	91	13.6	1.8	mesothyrid	2.5	2
26778	34.8	31.4		31.1	16.5	2.1	113	21	2.1	mesothyrid	3	2.5
26779	29.8	26.9	12.5	27.4	14.4	2	114	16.8	1.6	mesothyrid	3	1
26780	26.1	23.4	10.2	23.5	14	2	111	13.8	1.4	mesothyrid	2.5	0.5
26783	*24.3*	*22.2*	10.4	23.1	12.8	1.4	108	14.4	1.1	mesothyrid	2	

Maerewhenua River

Italicised entries are approximate due to slight crushing of shell etc.

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
27695	39.2	35.1	20.4	36.4	22.2	2.1	111	22	2	mesothyrid	3	3
27696	44.3	39.9	24.6	42.3	22	2.2	118	25.3	1.6	mesothyrid	3	2.5
27697	40.7	37.3	19.7	35.6	20.2	2.3	116	22.6	1.9	mesothyrid	2	3
27698	*40.8*	*37.2*	19.7	36	23	2	103	18	2	mesothyrid	3	2.5
27699	43.1	39		38.3	23.1	2.3	114		2.4	mesothyrid		1.5
27700	35.2	32	15	33.6	16.5	1.9	117	22	*1.6*	mesothyrid	2	0.5
27701	40	36.2	20.8			1.6	110		2.3	permesothyrid	3	3.5
27702	39	36.1	18.8	34.4	*20.1*	1.7	115	22.9	2.1	mesothyrid	2	2
27703	*39.6*	*35.5*	20.3	36.5	23.2	2.3	109	23.5	1.8	mesothyrid	3	2
27704			16.6	32.8	18.3	1.8	122	20.5	1.9	permesothyrid	2	
27705	37.8	34	21	35.1	19.2	2.1	104	22	1.4	mesothyrid	3.5	3
27706	37.6	34.4	19.6	34.6	20.1	2	111	21	1.7	mesothyrid	3	3
27707	35.8	32.6	18.5	33.5	18.4	1.7	117	20.1	2.1	mesothyrid	2.5	2.5
27708	36.5	32.5	18.4	32.4	19.1	2.4	114	22.2	1.7	mesothyrid	3	3
27709	31.1	27.9	16.4	32.7	16.7	1.8	118	20.1	1.9	mesothyrid	2.5	2
27710	35.4	32	16.6	31.7	18	2	115	21.2	1.5	mesothyrid	3	2.5
27712	30.4	27.5	14.6	29.6	15.3	1.7	117	18	1.8	mesothyrid	2	0.5
27713	31.1	27.5	15.8	28.9	15.5	1.8	116	18.3	1.9	mesothyrid	3	2

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
27714			15.5	*32.4*	17.3	1.8	125	19.1	1.8	mesothyrid	2	
27715	39.6	36.1	*25.2*	37.6	20.7	1.9	112	21.9	2	mesothyrid	3	2.5
27716	39.6	36.2	20.2	35	20.4	2.2	104	21.3	1.6	mesothyrid	3	2
27717	38.3	34.7	17.8	36.8	21	2	119	21.6	2	mesothyrid	2.5	2
27718	39.2	35.8	*18.8*	35.1	21.1	1.9	105	17.8	2	mesothyrid	2.5	1
27719	38	34.1	18.7	37.2	19.2	2.2	118	23.7	2.2	mesothyrid	3	2
27720	37	33.6	19.6	32.8	19.7	1.8	109	18.9	1.8	mesothyrid	3	3
27721	38.3	34.3	17.9	36.8	20.4	2.7	123	26.6	1.7	mesothyrid	3	1
27722	35	31.8	19	32.5	20.4	1.9	102	19	2.1	mesothyrid	2.5	1.5
27723	34.3	31.3	17.6	31.4	18.3	1.9	109	16.6	1.9	mesothyrid	3	2
27724	34.5	31.5	*15.5*	34.7	19	2	123	21	2	mesothyrid	2	2
27725	37.7	33.9	18.1	33.9	20	2.2	109	20		mesothyrid	3	2
27726			16.6			2.1	120	21.4	2	mesothyrid	2	
27727	33.5	30.4	17.5	29.1	16.6	1.9	108	18.7	1.9	mesothyrid	3	3
27728	31.9	29	15	29.1	16.3	1.9	116	20.2	1.6	mesothyrid	3	2.5
27729						1.7	108	18.3	2	mesothyrid	3	
27730	34	31	16.9	30.7	16.6	2.1	120	19.2	1.6	mesothyrid	2.5	1.5
27731						2.6	126		1.8	mesothyrid	3	
27732	34	31	18	30.5	17	1.4	111	17.2	1.7	mesothyrid	3	
27733	31.3	28.1	18.6	28.9	17	2	120	19.9	1.8	mesothyrid	2.5	2.5
27734	32	29	15.7	30.5	17.2	2.1	115	17.4	1.4	mesothyrid	3	3
27735	31	27.9	16.5	*27*	*15.8*	1.9	113	17.8	1.4	mesothyrid	3	2.5
27736	33.6	30.3	17.7	29.1	17.2	1.9	117	18.6	1.2	mesothyrid	3	2
27737	28.8	25.7	*14.4*	29.7	16.1	1.7	120	18.6	1.6	mesothyrid	3	2.5
27738	31.4	28.5	17.1	26.9	17.3	1.7	106	16.1	1.9	mesothyrid	3	0
27739	25.7	23.2	13.1	23.9	14.1	1.7	102	11.3		mesothyrid	3	2.5

Doherty's Quarry

Italicised entries are approximate due to slight crushing of shell etc.

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
1357	42.2	38	22.4	33.9	21.7	3.1	117	25.4	1.8	mesothyrid	2	2
1359	45.9	41.5	25.5	37.3	23.7	2.5	111	26.8	1.9	mesothyrid	3	2
1362	45.5	41.8	19	43.2	19.9	2.6	123	29.1		mesothyrid	2	2
1364	53.2	48.5	29.5	41	26.8	1.3	116	29	1.4	mesothyrid	3.5	2
1365	52.5	48.2	28.8	42.8	28.3	2.6	109	27.8	1.8	mesothyrid	3	2.5
1366	39.1	34.4	21.1	31.9	18.7	2.7	109	25.7	1.5	mesothyrid	3	1

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
1367	43.8	38.9	24.4	36.6	23.3	3	115	25.6	1.6	mesothyrid	3	2.5
1368	41.1	36.9	22	33.1	20.9	2.8	119	23.6	1.6	mesothyrid	3	1
1371	42.7	38.4	23.8	38.2	22.3	2.1	123	26.6	1.9	mesothyrid	3	1.5
1405	51.7	47	27.1	47.2	26.7	2.4	125	35.7	2	mesothyrid	3	2
1407	52.1	46.7	31.4	47.6	27.1	23	113	32.2		mesothyrid	3	1.5
1408	50.1	44.9	29.2	43.4	27.6	2.9	106	29.6		mesothyrid	3.5	2
1414	31	26.9	*13.6*	22.7	16.5	3.4	85	17.1		mesothyrid	2	0
1416	48.7	44.2	27.8	44	26.3	2.1	123	32.8	1.8	mesothyrid	3	2
1417	50	45.5	27.1	47	26.2	2.4	122	30.9		mesothyrid	3	1
1418	54	49.4		45.6	29.7	2	113	28.3		mesothyrid	3.5	2
1420	48.7	44	29.4	43.8	25.9	2.3	118	30.6		mesothyrid	3	2
1424	53.8	48.8	*31.1*	45.8	26.4	2.1	106	30.4	1.8	mesothyrid	3.5	2.5
1425	49.2	44.9	30	43.8	25	1.9	114	31	1.9	mesothyrid	4	1
1429	39.5	34.7	22.2	34.8	22.2	3	96	24.9		mesothyrid	2	0.5
1433	45.2	41.1		38.2	24.6	2.4	109	25.2	1.8	mesothyrid	3	2.5
1437	55.1	50.2	33.9	50.6	29.5	1.9	118	32.9	1.9	mesothyrid	3	1.5
1441	46.7	42.5	27.9	37.5	22.9	2.5	120	23.9		mesothyrid	3	2.5
1447	51	46.6	27.4	39.7	26.1	2.2	119	25	2	mesothyrid	3	3
1449	50.4	46	30.2	39.6	25.5	2.3	118	25.3	1.9	mesothyrid	3	4
1450	52.2	47.8	25.5	49.1	26.4	2.4	124	33.6		mesothyrid	2.5	3
1451	51.1	46.2	27.6	43.6	26.4	2.9	122	30.4	1.6	mesothyrid	3	2
1454	46.6	42.4	24.1	40.9	23.1	2.5	124	28.6	1.8	mesothyrid	3	2.5
1547	47.8	43.7	25	42.2	25.6	2.2	109	25.2		mesothyrid	3	1
1548	49.5	45	26.5	43.1	27.5	2.7	104	25.9		mesothyrid	3	1

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
1551	45.8	41	24.4	39.3	23.1	2.9	111	28.1	1.5	mesothyrid	3	2
1552	40.1	35.6	23.1	38.5	20.6	2.3	116	29.1		mesothyrid	3	2
1556	43.6	39.6	26.4	42.3	22.2	2.3	116	28.2	1.5	mesothyrid	3	2
1557	52.2	47.7	30.9	44.4	29.8	2.3	111	*28*	1.8	mesothyrid	3	2
1558	16.8	42.6	*26.1*	*46*	23	2.2	117	27.7	2	mesothyrid	3	1.5
1560	*57*	51.8	34.6	46.1	30.2	1.7	118	36.1	1.8	mesothyrid	3.5	2
29267	44.8	40.7	23.7	37.9	23.7	2.5	115	26.3	2.2	mesothyrid	2	2
29268	42.6	38.4				2.4	107		1.3	mesothyrid	3.5	*2.5*
29275	42.6	38.3	20	34.5	23.7	2.9	100	23.2	1.7	mesothyrid	2.5	2
29276	44.6	40.9	23.7	35.6	22.7	2.3	119			mesothyrid	3	2
29278	43.4	39.5		34.4	22.1	2	119	26	1.5	mesothyrid	3	2.5
29280			23.5			2.7	125	*28.4*	1.6	mesothyrid	2	
29281	46.3	41.9		38	23.3	2	117	24.4	1.1	mesothyrid	3	3
29282			22.9	36	22.2	2.4	108	26		mesothyrid	3	
29283	40	35.7	21.5	30.7	22	2.9	96	22.1	2.2	mesothyrid	2.5	2
29284	42.8	38.7	24.4	35.5	24.4	2.4	121	23.9	2.1	mesothyrid	3	*3*
29287	43.6	39.4	*25.3*			2.8	122	24.2		mesothyrid	3	*1*
29288	47.3	42.7	20.7	38.1	25.1	2.7	114	23.6	2	mesothyrid	2.5	2
29289	41.3	37.3	27.5	32.9	21.8	2.4	121	23.2	1.4	mesothyrid	3	3.5
29290	43.9	39.2				2.3	109	26.9	1.5	mesothyrid	3	*1*
29291	31.4	30.4	17.7	28.3	15.3	1.8	112	20.2	1.1	mesothyrid	3	2.5
29292			21.5	30.8	22.2	2.2	121	22.9		mesothyrid	2.5	
29300				41.5	24.5	2.6	124		1.7	mesothyrid		
29301				30	15.2	2.3	116	*20.2*		mesothyrid	3	
29302			26.2	40.4	25	2.8				mesothyrid	3	2
26429			30.4	*41.5*								3.5
26434	48.7	44.5	26.1	41.5	26.1	2.6	124	25.3	1.5	mesothyrid	3.5	2.5
26435	46.4	41.9	*27.5*	39.5	25.1	2.8	121	28.3	2.2	mesothyrid	2	2.5
26437	47.3	*42.8*		35.7	25.8	2.8	115	27		mesothyrid	3	1.5

Allan No.	Length v	Length d	Thickness max.	Width max.	Lth. v@Wmax.	Lth. Card. Area	Beak Angle	"Hinge Length"	Foramen D.	Foramen Type	Beak Curvature	Sulcation Index
26440	44.3	40.7		36.1	25.4	2.4	116	26.1		mesothyrid	3	2.5
26441	42.4			35.2	23.4					mesothyrid		2.5
26442			25			2.2	119	27	1.5	mesothyrid	3	
26444	44.1	39.9		30.3	23.8	2.2	112			mesothyrid	3	3
26446	40.9	36.5	22.5	33	21.6	2.7	126	2.54	1.4	mesothyrid	3	3
26449	41.9	38.2	19.7	34.1	21	2.6	125		1.3	mesothyrid	2	2
26450				32.6	20.6	2.1	121	23.7	1.2	mesothyrid	3	
26451	41	37.1		34.1	24.6	2.4	107	21.5	1.8	mesothyrid	2.5	2
26455	35.7	32.3		32.8	14.6	2.5	123	25.2		mesothyrid	3	1
26457	32.6	29.3	16.5	31	14.8	2.1	117	21.9	1.5	mesothyrid	2.5	1

REFERENCES

ALDRIDGE, A. E., 1981, Intraspecific variation of shape and size in subtidal populations of two Recent New Zealand articulate brachiopods. *New Zealand Journal of Zoology 8*, p. 169-174

ALDRIDGE, A. E., 1990, Shape variation of Neothyris (Brachiopoda, Terebratellinae), p. 115-122 *in* MacKinnon, D. I., Lee, D. E., & Campbell, J. D. (eds.), 1991, q.v.

ALLAN, R. S., 1927, The geology and paleontology of the lower Waihao Basin, South Canterbury, New Zealand. *Transactions and Proceedings of the New Zealand Institute 57*, p. 265-309

ALLAN, R. S., 1931, Description of Tertiary Brachiopoda from New Zealand, Part I. *Transactions and Proceedings of the New Zealand Institute 62 (2)*, p. 156-160, pl. 20-22

ALLAN, R. S., 1932, Tertiary Brachiopoda from the Chatham Islands, New Zealand. *Transactions and Proceedings of the New Zealand Institute 63 (1)*, p. 11-23, pl. 4-6

ALLAN, R. S., 1933, On the system and stage names applied to subdivisions of the Tertiary strata in New Zealand. *Transactions and Proceedings of the New Zealand Institute 63 (2)*, p. 81-108

ALLAN, R. S., 1937a, Type Brachiopoda in the Canterbury Museum. *Records of the Canterbury Museum 4 (3)*, p. 115-128, pl. XV-XVI

ALLAN, R. S., 1937b, Two new Hutchinsonian (Tertiary) brachiopods from New Zealand. *Records of the Canterbury Museum 4 (3)*, p. 129-130, pl. XVII

ALLAN, R. S., 1937c, Tertiary Brachiopoda from the Mount Brown beds of Mount Donald, Weka Pass district, New Zealand. *Records of the Canterbury Museum 4 (3)*, p. 131-137, pl. XVIII

ALLAN, R. S., 1937d, Tertiary Brachiopoda from the Forest Hill Limestone (Hutchinsonian) of Southland, New Zealand. *Records of the Canterbury Museum 4 (3)*, p. 139-153, pl. XIX-XX

ALLAN, R. S., 1938a, Palaeontology, p. 60-63 *in* Speight, R., 1938, q.v.

ALLAN, R. S., 1938b, The Duntroonian Stage: a new division of the Oamaruian system, p. 89-92, Appendix *in* Speight, R., 1938, q.v.

ALLAN, R. S., 1940, Studies on the Recent and Tertiary Brachiopoda of Australia and New Zealand. Part II, *Records of the Canterbury Museum 4 (6)*, p. 277-297, pl. XXXV-XXXVII

ALLAN, R. S., 1949, Notes on a comparison of the Tertiary and Recent Brachiopoda of New Zealand and South America. *Transactions and Proceedings of the Royal Society of New Zealand 77 (5)*, p. 288-289

ALLAN, R. S., 1957, Appendix 3: Brachiopod faunas, p. 104-107 *in* Gage, M., 1957, q.v.

ALLAN, R. S., 1960, The succession of Tertiary brachiopod faunas in New Zealand. *Records of the Canterbury Museum 7 (3)*, p. 233-268

ALLAN, R. S., 1963, comments, p. 47 *in* Fleming, C. A., 1963, q.v.

ANDREW, A. R., 1906, On the geology of the Clarendon phosphate deposits, Otago, New Zealand. *Transactions of the New Zealand Institute 38*, p. 447-482, pl. IV-VIII

BELLISS, S. E., 1978, The palaeoecology of the Otekiake Limestone. Unpublished MSc. thesis, University of Canterbury Library

BIERNAT, G., BIRKENMAJER, K., & POPIEL-BARCZYK, E., 1985, Tertiary brachiopods from the Moby Dick Group of King George Island (South Shetland Islands, Antarctica). *Studia Geologica Polonica 81 (5)*, p. 109-141, pl. I-XII

BOWEN, Z. P., & CAMPBELL, J. D., 1973, Systematics and evolution of the brachiopod genus *Rhizothyris* in the Oligocene-Miocene of New Zealand. *Journal of the Royal Society of New Zealand 3 (2)*, p. 141-160

BROWNE, G. H., & FIELD, B. D., 1985, The lithostratigraphy of late Cretaceous to early Pleistocene rocks of northern Canterbury, New Zealand. *New Zealand Geological Survey Record 6*, p. 1-64, 15 figs.

BUCKMANN, S. S., 1910, Antarctic fossil Brachiopoda collected by the Swedish South Polar Expedition. *Wissenchaftliche Ergebnisse der Schwedischen Südpolar expedition, 1901-1903, 3 (7)*, p. 1-40, 3 pl.

CHAPMAN, B. E., & RICHARDSON, J. R., 1981, Recent species of *Neothyris* (Brachiopoda : Terebratellinae), *New Zealand Journal of Zoology 8 (2)*, p. 157-161

COHEN, B. L., BALFE, P., COHEN, M., & CURRY, G. B., 1990, Genetic divergence within and between populations of the North Atlantic morphospecies *Terebratulina retusa* and *T. septentrionalis*, p. 109-114 *in* MacKinnon, D. I., Lee, D. E., & Campbell, J. D. (eds.), 1991, q.v.

COOPER, R. A., 1966, Limestone Resources of the Otago Area. *New Zealand Geological Survey Report 15*, Department of Scientific and Industrial Research, New Zealand, p. 1-67, 11 figs.

DAWSON, E. W., 1990a, The Cenozoic Brachiopoda of New Zealand: A commentary, reference list, and bibliography. New Zealand Oceanographic Institute Division of Water Sciences, Department of Scientific and Industrial Research miscellaneous publication 103, p. 1-99

DAWSON, E. W., 1990b, The systematics and biogeography of the living brachiopoda of New Zealand, p. 431-437 *in* MacKinnon, D. I., Lee, D. E., & Campbell, J. D. (eds.), 1991, q.v.

ENDO, K., & CURRY, G. B., 1990, Molecular and morphological taxonomy of a Recent brachiopod genus *Terebratulina*, p. 101-108 *in* MacKinnon, D. I., Lee, D. E., & Campbell, J. D. (eds.), 1991, q.v.

FIELD, B. D., & BROWNE, G. H., 1986, Lithostratigraphy of Cretaceous and Tertiary rocks, southern Canterbury, New Zealand. *New Zealand Geological Survey Record 14*, p. 1-56, 12 figs.

FINLAY, H. J., 1939a, New Zealand Foraminifera : Key Species in Stratigraphy No. 1. *Transactions of the Royal Society of New Zealand 68*, p. 504-533, pl. 68-69

FINLAY, H. J., 1939b, New Zealand Foraminifera : Key Species in Stratigraphy, No. 2. *Transactions of the Royal Society of New Zealand 69*, p. 89-128, pl. 11-14

FINLAY, H. J., 1939c, New Zealand Foraminifera : Key Species in Stratigraphy, No. 3. *Transactions of the Royal Society of New Zealand 69*, p. 309-329, pl. 24-29

FINLAY, H. J., 1940, New Zealand Foraminifera : Key Species in Stratigraphy No. 4. *Transactions of the Royal Society of New Zealand 69*, p. 448-472, pl. 62-67

FINLAY, H. J., 1947, New Zealand Foraminifera : Key Species in Stratigraphy No. 5. *New Zealand Journal of Science and Technology B28 (5)*, p. 259-292, pl. 1-9

FINLAY, H. J., & MARWICK, J., 1940, The divisions of the Upper Cretaceous and Tertiary in New Zealand. *Transactions of the Royal Society of New Zealand 70 (1)*, p. 77-135

FINLAY, H. J., & MARWICK, J., 1947, New Divisions of the New Zealand Upper Cretaceous and Tertiary. *New Zealand Journal of Science and Technology B28 (4)*, p. 228-236

FLEMING, C. A., 1963, Macrofossils, p. 33, 39-40, 46-49, 52-57, of Chapter 4 *in* Wilson, D. D., 1963, q.v.

FLEMING, C. A., HORNIBROOK, N de B., & WOOD, B. L., 1969, Chapter 4 *in* Wilson, B. L., 1969, q.v.

FORDYCE, R. E., 1996, Cenozoic Geology of North Otago and South Canterbury. *Geological Society of New Zealand Field Trip Guide FT7*, p. 1-8

FORDYCE, R. E., HORNIBROOK, N. de B., & MAXWELL, P. A., 1985, Cenozoic of North Otago and South Canterbury. Hornibrook Symposium, Christchurch, New Zealand, December 1985. Association of Australasian Paleontologists/Geological Society of New Zealand. Guide Book No. 2, Field Trip Guide to Cenozoic Geology of North Otago and South Canterbury. *Geological Society of New Zealand Miscellaneous Publication 33B*, p. 1-50

FOSTER, M. W., 1974, Recent Antarctic and Subantarctic brachiopods. *Antarctic Research Series 21*, American Geophysical Union, Washington, D. C., p. 189

FOSTER, M. W., 1989, Brachiopods from extreme South Pacific and adjacent waters. *Journal of Paleontology 63 (3)*, p. 268-301, 17 figs.

GAGE, M., 1957, The Geology of Waitaki Subdivision. *Bulletin, New Zealand Geological Survey n.s. 55*, p. 1-135, 4 maps

GAGE, M., 1970, Late Cretaceous and Tertiary rocks of Broken River, Canterbury. *New Zealand Journal of Geology and Geophysics 13 (2)*, p. 507-559

GHOSH, D. N., 1990, Biometry of two species of *Kallirhynchia* (Buckman) from Callovian beds, p. 97-100 *in* MacKinnon, D. I., Lee, D. E., & Campbell, J. D. (eds.), 1991, q.v.

HATAI, K., 1965, Generic description of *Waiparia* Thomson, p. 855 *in* Muir-Wood, H. M., Elliot, G. F., & Hatai, K., 1905, q.v.

HORNIBROOK, N de B., 1982, Guide Book for Tour BW 12 (B13), Upper Eocene, Oligocene and Lower Miocene biostratigraphy of North Otago and South Canterbury. *15th Pacific Science Congress and 3rd International Meeting on Pacific Neogene Stratigraphy*, Dunedin, 1983, p. 19

HORNIBROOK, N de B., BRAZIER, R. C., & STRONG, C. P., 1989, Manual of New Zealand Permian to Pleistocene Foraminiferal Biostratigraphy. *New Zealand Geological Survey Paleontological Bulletin 56*, p. 175

HOSKINS, G. H. (ed.), 1982, Stages of the New Zealand marine Cenozoic : A synopsis. *Report, New Zealand Geological Survey 107*, p. 1-74

HUTTON, F. W., 1873, Catalogue of the Tertiary Mollusca and Echinodermata of New Zealand, in the Collection of the Colonial Museum, Colonial Museum and Geological Survey Department Government Printer, Wellington, p. xx + 1-116, 1 pl.

HUTTON, F. W., 1905, Revision of the Tertiary Brachiopoda of New Zealand. *Transactions and Proceedings of the New Zealand Institute 37*, p. 474-481, pl. XLV-XLVI

HYDEN, F. M., 1979, Mid-Tertiary Temperate Shelf Bioclastic Limestones, Southland, New Zealand. Unpublished PhD. thesis, University of Otago Library

IHERING, H. von, 1903, Les brachiopodes Tertiaires de Patagonie. *Anales del Museo nacional Buenos Aires IX (ser. 3a, T. II)*, p. 321-241, pl. III

KEYES, I. W., 1971, Type specimens of New Zealand Cenozoic invertebrates in the Dominion Museum. *Records of the Dominion Museum 7 (9)*, p. 65-84

LEE, D. E., 1978a, Cenozoic and Recent rhynchonellide brachiopods of New Zealand : Genus *Aetheia*. *Journal of the Royal Society of New Zealand 8 (1)*, p. 93-113

LEE, D. E., 1978b, Aspects of the ecology and paleoecology of the brachiopod *Notosaria nigricans* (Sowerby). *Journal of the Royal Society of New Zealand 10 (2)*, p. 137-144

LEE, D. E., 1980, Cenozoic and Recent rhynchonellide brachiopods of New Zealand : Systematics and variations in the genus *Tegulorhynchia*. *Journal of the Royal Society of New Zealand 10 (3)*, p. 223-245

LEE, D. E., 1990, Cenozoic brachiopod faunas of North Otago, Field Trip Guide N73, Second International Brachiopod Congress, *Geological Society of New Zealand miscellaneous publication 46B*, p. 1-23

LEE, D. E., FORDYCE, E., & MAXWELL, P., 1996, Cenozoic geology of North Otago and South Canterbury, Field Trip Guide FT7, Geological Society of New Zealand Annual Conference 1996, *Geological Society of New Zealand miscellaneous publication 91B*, p. FT7–1- FT7–20

LEE, D. E., & WILSON, J. B., 1979, Cenozoic and Recent rhynchonellide brachiopods of New Zealand : Systematics and variation in the genus *Notosaria*. *Journal of the Royal Society of New Zealand 9 (4)*, p. 437-463

LEVY, R., 1961, Sobre algunos Terebratellidae de Patagonia (Argentina). *Ameghiana 2 (5)*, p. 79-88, pl. 1-4

LEWIS, D. W., & BELLISS, S. E., 1984, Mid Tertiary unconformities in the Waitaki Subdivision, North Otago. *Journal of the Royal Society of New Zealand 14 (3)*, p. 251-276

McCULLOCH, B. A., 1981, Geology of the Mount Brown beds. Unpublished Msc. thesis, University of Canterbury Library

McKINNEY, M. L., & McNAMARA, K. J., 1991, Heterochrony : The Evolution of Ontogeny. Plenum Press, New York, p. 437

MacKINNON, D. I., LEE, D. E., & CAMPBELL, J. D. (eds.), 1991, Brachiopods through Time. A. A. Balkema, Rotterdam, p. xi + 1-447

MacKINNON, D. I., BEUS, S. S., & LEE, D. E., 1993, Brachiopod fauna of the Kokoamu Greensand (Oligocene), New Zealand. *New Zealand Journal of Geology and Geophysics 36*, p. 327-347

MAYR, E., 1970, Populations, Species, and Evolution. Harvard University Press, Cambridge, Mass.

MINEUR, R. J., & RICHARDSON, J. R., 1984, Free and mobile brachiopods from New Zealand Oligocene deposits and Australian waters. *Alcheringa 8*, p. 327-334

MOORE, R. C. (ed.), 1965, Treatise on Invertebrate Paleontology, Part H, Brachiopoda. Volume 2. Geological Society of America, New York, University of Kansas, Lawrence, p. ii + 523-927

MUIR-WOOD, H. M., ELLIOT, G. F., & HATAI, K., 1965, Mesozoic and Cenozoic Terebratellidina, p. H816-H857, *in* Moore, R. C. (ed.), 1965, q.v.

OWEN, E. F., 1980, Tertiary and Cretaceous brachiopods from Seymour, Cockburn and James Ross Islands, Antarctica. *Bulletin of the British Museum of natural History 33 (2)*, p. 123-145

PARK, J., 1905, On the marine Tertiaries of Otago and Canterbury, with special reference to the relations existing between the Pareora and Oamaru Series. *Transactions and Proceedings of the New Zealand Institute 37*, p. 489-551, pl. LVIII

PARK, J., 1918, The geology of the Oamaru district, North Otago (eastern Otago division). *New Zealand Department of Mines, Geological Survey Branch, Bulletin n.s. 20*, p. viii + 1-124, 3 maps, 3 sections, pl. I-XII

PARK, J., 1921, Geology and mineral resources of western Southland. *New Zealand Department of Mines, Geological Survey Branch, Bulletin n.s. 23*, p. vi + 1-88, pl. I-VIII, maps

RICHARDSON, J. R., 1979, Pedicle structure of articulate brachiopods. *Journal of the Royal Society of New Zealand 9 (4)*, p. 415-436

RICHARDSON, J. R., 1981a, Brachiopods and pedicles. *Paleobiology 7 (1)*, p. 87-95

RICHARDSON, J. R., 1981b, Recent brachiopods from New Zealand – background to the study cruises of 1977-79. *New Zealand Journal of Zoology 8*, p. 133-143

RICHARDSON, J. R., 1981c, Distribution and orientation of six articulate brachiopod species from New Zealand. *New Zealand Journal of Zoology 8*, p. 189-196

RICHARDSON, J. R., 1987, Brachiopods from carbonate sands of the Australian shelf. *Proceedings of the Royal Society of Victoria 99 (1)*, p. 37-50

SCHUMANN, D., 1990, Hydrodynamic influences in brachiopod shell morphology of *Terebratalia transversa* (Sowerby) from the San Juan Islands, USA, p. 265-271 *in* MacKinnon, D. I., Lee, D. E., & Campbell, J. D. (eds.), 1991, q.v.

SCOTT, G. H., 1971, Revision of Hutchinsonian, Awamoan, and Altonian Stages (Lower Miocene, New Zealand) – 1. *New Zealand Journal of Geology and Geophysics 14 (4)*, p. 705-726

SCOTT, G. H., 1972, Revision of Hutchinsonian, Awamoan and Altonian Stages (Lower Miocene, New Zealand) – 2. *New Zealand Journal of Geology and Geophysics 15 (1)*, p. 49-70

SCOTT, G. H., 1980, The value of Outline Processing in the Biometry and Systematics of fossils. *Palaeontology 23 (4)*, p. 757-768

SHEA, B.T., 1988, Heterochrony in primates, *in* McKinney, M. L., (ed.), 1990, Heterochrony in Evolution : A Multidisciplinary Approach. Plenum Press, New York

SPEIGHT, R., 1938, The geology of the Mount Somers district. *New Zealand Department of Scientific and Industrial Research Geological Memoir 3*, p. 1-116, 1 map, 9 sections

STEWART, I. R., 1981, Population structure of articulate brachiopod species from soft and hard substrates. *New Zealand Journal of Zoology 8*, p. 197-207

TATE, R., 1880, On the Australian Tertiary palliobranchs. *Transactions of the Royal Society of South Australia 3*, p. 140-170, pl. VII-XI

THOMSON, J. A., 1908, Fossils from Kakanui. *Transactions and Proceedings of the New Zealand Institute 40*, p. 98-103, pl. XIV

THOMSON, J. A., 1915, Brachiopod genera : the position of shells with magaselliform loops, and of shells with bouchardiform beak characters. *Transactions and Proceedings of the New Zealand Institute 47*, p. 302-403

THOMSON, J. A., 1916, On the stage names applicable to the divisions of the Tertiary in New Zealand. *Transactions and Proceedings of the New Zealand Institute 48*, p. 28-40

THOMSON, J. A., 1917, Diastrophic and other considerations in classification and correlation, and the existence of minor diastrophic districts in the Notocene. *Transactions and Proceedings of the New Zealand Institute 49*, p. 397-413

THOMSON, J. A., 1918a, Appendix 3 : Brachiopoda, p. 117-119 *in* Park, J., 1918, q.v.

THOMSON, J. A., 1918b, On the age of the Waikouaiti Sandstone. *Transactions and Proceedings of the New Zealand Institute 50*, p. 196-197

THOMSON, J. A., 1918c, Brachiopod identifications *in* Gudex, M. C., 1918, The succession of Tertiary beds in the Pareora district, South Canterbury. *Transactions and Proceedings of the New Zealand Institute 50*, p. 244-262, pl. XVI-XVII

THOMSON, J. A., 1920, The Notocene geology of the Middle Waipara and Weka Pass district, North Canterbury, New Zealand. *Transactions and Proceedings of the New Zealand Institute 52*, p. 322-415, pl. XVI-XXVII

THOMSON, J. A., 1926, Marine phosphatic horizons in the Tertiary limestones and greensands of South Canterbury and North Otago, and brachiopod evidence as to their age. *New Zealand Journal of Science and Technology 8 (3)*, p. 143-160

THOMSON, J. A., 1927, Brachiopod Morphology and Genera (Recent and Tertiary). New Zealand Board of Science and Art, Manual No. 17. Government Printer, Wellington, p. vi + 1-338, pl. 1-2

TOHA, B., 1993, Stratigraphy and sedimentation of the Caversham Formation. Unpublished Msc. thesis, University of Otago Library

WILLETT, R. W., 1950, The Limestone Resources of Southland. *Bulletin of the New Zealand Geological Survey n.s. 49*, p. i + 1-43

WILSON, D. D., 1963, Geology of Waipara Subdivision. *Bulletin, New Zealand Geological Survey n.s. 64*, p. 1-122, 4 maps

WOOD, B. L., 1969, Geology of Tuatapere Subdivision, Western Southland. *Bulletin of the New Zealand Geological Survey n.s. 79*, p. 1-162, 2 maps

WULFF, J. I., 1990, Intraspecific morphologic variability in *Spirifer pellaensis*, Greenbrier Group (Upper Mississippian/Lower Carboniferous), USA, p. 49-56 *in* MacKinnon, D. I., Lee, D. E., & Campbell, J. D. (eds.), 1991, q.v.

Transactions and Proceedings of the New Zealand Institute 37, p. 489-551, pl. LVIII

PARK, J., 1918, The geology of the Oamaru district, North Otago (eastern Otago division). *New Zealand Department of Mines, Geological Survey Branch, Bulletin n.s. 20*, p. viii + 1-124, 3 maps, 3 sections, pl. I-XII

PARK, J., 1921, Geology and mineral resources of western Southland. *New Zealand Department of Mines, Geological Survey Branch, Bulletin n.s. 23*, p. vi + 1-88, pl. I-VIII, maps

RICHARDSON, J. R., 1979, Pedicle structure of articulate brachiopods. *Journal of the Royal Society of New Zealand 9 (4)*, p. 415-436

RICHARDSON, J. R., 1981a, Brachiopods and pedicles. *Paleobiology 7 (1)*, p. 87-95

RICHARDSON, J. R., 1981b, Recent brachiopods from New Zealand – background to the study cruises of 1977-79. *New Zealand Journal of Zoology 8*, p. 133-143

RICHARDSON, J. R., 1981c, Distribution and orientation of six articulate brachiopod species from New Zealand. *New Zealand Journal of Zoology 8*, p. 189-196

RICHARDSON, J. R., 1987, Brachiopods from carbonate sands of the Australian shelf. *Proceedings of the Royal Society of Victoria 99 (1)*, p. 37-50

SCHUMANN, D., 1990, Hydrodynamic influences in brachiopod shell morphology of *Terebratalia transversa* (Sowerby) from the San Juan Islands, USA, p. 265-271 *in* MacKinnon, D. I., Lee, D. E., & Campbell, J. D. (eds.), 1991, q.v.

SCOTT, G. H., 1971, Revision of Hutchinsonian, Awamoan, and Altonian Stages (Lower Miocene, New Zealand) – 1. *New Zealand Journal of Geology and Geophysics 14 (4)*, p. 705-726

SCOTT, G. H., 1972, Revision of Hutchinsonian, Awamoan and Altonian Stages (Lower Miocene, New Zealand) – 2. *New Zealand Journal of Geology and Geophysics 15 (1)*, p. 49-70

SCOTT, G. H., 1980, The value of Outline Processing in the Biometry and Systematics of fossils. *Palaeontology 23 (4)*, p. 757-768

SHEA, B.T., 1988, Heterochrony in primates, *in* McKinney, M. L., (ed.), 1990, Heterochrony in Evolution : A Multidisciplinary Approach. Plenum Press, New York

SPEIGHT, R., 1938, The geology of the Mount Somers district. *New Zealand Department of Scientific and Industrial Research Geological Memoir 3*, p. 1-116, 1 map, 9 sections

STEWART, I. R., 1981, Population structure of articulate brachiopod species from soft and hard substrates. *New Zealand Journal of Zoology 8*, p. 197-207

TATE, R., 1880, On the Australian Tertiary palliobranchs. *Transactions of the Royal Society of South Australia 3*, p. 140-170, pl. VII-XI

THOMSON, J. A., 1908, Fossils from Kakanui. *Transactions and Proceedings of the New Zealand Institute 40*, p. 98-103, pl. XIV

THOMSON, J. A., 1915, Brachiopod genera : the position of shells with magaselliform loops, and of shells with bouchardiform beak characters. *Transactions and Proceedings of the New Zealand Institute 47*, p. 302-403

THOMSON, J. A., 1916, On the stage names applicable to the divisions of the Tertiary in New Zealand. *Transactions and Proceedings of the New Zealand Institute 48*, p. 28-40

THOMSON, J. A., 1917, Diastrophic and other considerations in classification and correlation, and the existence of minor diastrophic districts in the Notocene. *Transactions and Proceedings of the New Zealand Institute 49*, p. 397-413

THOMSON, J. A., 1918a, Appendix 3 : Brachiopoda, p. 117-119 *in* Park, J., 1918, q.v.

THOMSON, J. A., 1918b, On the age of the Waikouaiti Sandstone. *Transactions and Proceedings of the New Zealand Institute 50*, p. 196-197

THOMSON, J. A., 1918c, Brachiopod identifications *in* Gudex, M. C., 1918, The succession of Tertiary beds in the Pareora district, South Canterbury. *Transactions and Proceedings of the New Zealand Institute 50*, p. 244-262, pl. XVI-XVII

THOMSON, J. A., 1920, The Notocene geology of the Middle Waipara and Weka Pass district, North Canterbury, New Zealand. *Transactions and Proceedings of the New Zealand Institute 52*, p. 322-415, pl. XVI-XXVII

THOMSON, J. A., 1926, Marine phosphatic horizons in the Tertiary limestones and greensands of South Canterbury and North Otago, and brachiopod evidence as to their age. *New Zealand Journal of Science and Technology 8 (3)*, p. 143-160

THOMSON, J. A., 1927, Brachiopod Morphology and Genera (Recent and Tertiary). New Zealand Board of Science and Art, Manual No. 17. Government Printer, Wellington, p. vi + 1-338, pl. 1-2

TOHA, B., 1993, Stratigraphy and sedimentation of the Caversham Formation. Unpublished Msc. thesis, University of Otago Library

WILLETT, R. W., 1950, The Limestone Resources of Southland. *Bulletin of the New Zealand Geological Survey n.s. 49*, p. i + 1-43

WILSON, D. D., 1963, Geology of Waipara Subdivision. *Bulletin, New Zealand Geological Survey n.s. 64*, p. 1-122, 4 maps

WOOD, B. L., 1969, Geology of Tuatapere Subdivision, Western Southland. *Bulletin of the New Zealand Geological Survey n.s. 79*, p. 1-162, 2 maps

WULFF, J. I., 1990, Intraspecific morphologic variability in *Spirifer pellaensis*, Greenbrier Group (Upper Mississippian/Lower Carboniferous), USA, p. 49-56 *in* MacKinnon, D. I., Lee, D. E., & Campbell, J. D. (eds.), 1991, q.v.